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THE DEVELOPMENT AND EARLY ONTOGENY IN APHYOSEMION GARDNERI AND APHYOSEMION SCHEELI (PISCES: CYPRINODONTIDAE: RIVULINAE)

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Abstract. The development of two species of Cyprinodont fishes, i.e., *Aphyosemion gardneri* and *Aphyosemion scheeli*, was compared and described in detail. The development of *A. gardneri* is longer than that of *A. scheeli* under the same conditions. The scalation in both species is of caudo-oral type. In *A. gardneri* the possibility of the arrest in the stage of the long somite embryo (diapause II.) and than again in the pre-hatching stage (diapause III.) was confirmed.

INTRODUCTION

Both investigated species of cyprinodont fishes which originate from West Africa are quite common aquaria fishes. *Aphyosemion scheeli* was described and separed from *A. gardneri* (Boulenger, 1911) by Radda in 1970 only (Radda 1970), mainly on the basis of different caryotype, some morphological and meristic characters and coloration. In the popular literature the fish up to this time was known by the commercial name *Aphyosemion* "burundi". Different populations of *A. gardneri* are in the nature different as well in form as in colour and were described as subspecies, e.g. *A. g. nigerianum* Clausen, 1963, *A. g. lacustris* Radda, 1974, *A. g. manfens* Radda, 1974, *A. g. obuduense* Wright & Jeremy, 1974 (see Radda 1975). According to Radda (1970) is *A. scheeli* phylogenetical closely allied with *A. gardneri* and *A. santaisabellae*, as well as with *A. calliurum*.

Aphyosemion gardneri and *Aphyosemion scheeli* breed in aquarium willingly and the eggs are deposited in the bottom or in plants. During the spawning season, which in the nature may last the year round, the fishes spawn and produce a small number of eggs daily. According to Peters (1963), Scheel (1968) and Wourms (1972) *Aphyosemion gardneri* may be (sometimes?) annual, i.e. that the species can exist over the dry season in the eggs stage only (Myers 1942, 1952). (*A. gardneri* = *A. nigerianum* in Wourms = *A. calliurum* in Peters).

As to the developmental terminology of fishes we adopted those given by Balon (1969, 1975). More difficult is the question of definition of the stages of embryonal development. The stages given for *Fundulus heteroclitus* by Oppenheimer (1937) are not detailed enough and the very precisely defined stages given for *Austrofundulus myersi* by Wourms (1972 a) are suitable for strictly annual species only because the stages of complete dispersion and subsequent reaggregation of blastomeres are interponed between cleavage stage and embryogenesis. Therefore, I prefer to indicate the stages in our species by words and note the equivalent stages of Oppenheimer and Wourms for comparison only. It may be stressed out, however, that some

small differences against accepted terminology are present alike in both investigated species, before all in the late pre-hatching stage of the egg and the transition of the larval to the juvenile period.

MATERIAL AND METHODS

Two males and three females of *Aphyosemion gardneri* and one male and three females of *A. scheeli* were obtained from the local dealer. Each group spawned into nylon fibre in 30 × 16 × 16 cm all glass aquaria during 3 (*A. gardneri*) and 4 (*A. scheeli*) days. Water: 19—25 °C, pH = 6,3—6,5, °dGH about 7 (carbonate 2,43,° sulfate 4,7°). The fishes were set into aquarium at 16h and the eggs collected from the nylon fibre every following day at 7h. At all, 52 eggs from *A. gardneri* and 62 eggs from *A. scheeli* were collected and than water incubated in small petridishes placed in plastic boxes. The water of the same quality as above was used for incubation by the temperature 22—25 °C with the mean temperature 24 °C. One drop (about 0,04 ml) of 4% acriflavin was given to about 200 ml water (resulting concentration of acriflavin about 0,0008 %) to suppress the growth of microorganisms. The eggs were in the dark except for breef exposure to light during observation and manipulation. All observations were made in vivo in enlargement 24×, 48× and 144× in transmitted and reflected light. The larvae after hatching were studied under narcotization with 0,5 % solution of urethan (cf. Buddenbrock 1960). The recovering was quick and safe in all instances. During incubation 8 eggs of *A. gardneri* (15 %) and 5 eggs of *A. scheeli* (8 %) decayed.

OBSERVATIONS

Because of the method of egg-collecting the early cleavage stages of the eggs could not be studied in all instances. Obviously, the eggs were collected in various stages of activated eggs (stage 2 of Oppenheimer or Wourms) or of blastodisc development (stage 3 and 4 of Oppenheimer or stage 3 of Wourms). Some eggs were in the two cell stage or four cell stage (stages 4 and 5 of Wourms). The development from the stage of activated egg to the two cell stage lasted about 2,5 h, up to the four cell stage about 3.5 h. Therefore, we must assume that the spawning of the fishes took place in the early morning only. The further development was quite equal in both species in investigation. The stage 18 of Wourms (or stage 11 of Oppenheimer), i.e. three-fourth owergrowth of blastula, was reached after about 10 h and the stage 29 (stage 15—16 of Oppenheimer), i.e. early somite embryo, after 58 h. After reaching this stage the developing vary individually in the eggs. The total time of embryonal development is shown in the Table 1.

Our special attention deserves the egg of *A. gardneri* with the developing time of 58 days. In this egg the developmental arrest occured in the stage of the long somite embryo (stage 22 of Oppenheimer, stage 32—33 of Wourms or stage II. of Peters) at the age of 9 days. It is the obvious outstep of the diapause II. (Wourms 1972 b). The egg was arrested in this diapause for 28 days. After this period the eggs developed continuously to the 50th day, at which time it was in the pre-hatching stage. This was prolonged to 7 days and the egg hatched on 58th day.

In *Roloffia occidentalis*, the species related to *Aphyosemion*, the arrest in diapausa II. has a duration of up to 50 days (Wourms 1972 b), according to Scheel (1968) up to 100 days. In water-incubated eggs of *A. gardneri* arrest at stage 43 (pre-hatching stage) is sometimes present and is considered to be an instance of diapause III. (Wourms 1972). Our instance, however, confirms that in this species the diapause II. can be present as well (cf. Pe-

Table 1. The lasting of incubation in days.

A. gardneri		*A. scheeli*	
No. of days	No. of eggs	No. of days	No. of eggs
7	8	7	3
8	1	8	14
9	2	9	12
12	5	10	7
13	24	11	2
14	1	12	4
17	1	13	11
18	1	14	4
58	1	17	1
	total 44	18	2
		20	3
			total 57

ters 1963). Such eggs, which need much longer time to develope as other are well known to aquarists which name them "resting eggs" (cf. Roloff 1967). Unfortunately, we lack detail observation of such routinely incubated eggs. In the aquaristic routine the eggs of *A. gardneri* are often incubated as that of annual species (Weber 1970, Tresnak 1978) and the diapause is considered as arteficial subject to stress conditions (Scheel 1968. Wourms 1972 c).

Very interesting was the investigation of the heart frequences in embryos. After developing of simple tubular heart it beats average 40 min^{-1} and the heart-beats go up to 85—90 min^{-1} in the time of the branching of vena subvitellina (vena subintestinalis). Than, blood elements appear and the heart-beats slowed down to 65—67 min^{-1}. In the following days the heartbeats accelerate again up to about 110 min^{-1}, sometimes up to 150 min^{-1} (in *A. scheeli*) in the pre-hatching stage. The decreasing of the frequency of heartbeats in the period after branching of v. subintestinalis and with appearance of blood elements in the vessels noted Balon (1977) in *Labeotropheus*, too, but this phenomenon was apparently not observed in Lepomis gibbosus or Cichlasoma *nigrofasciatum* (Balon 1959, 1960).

In the "resting egg" of *A. gardneri* the heart on the beginning of the arrest in the diapausa II. beated 25 min^{-1}. At the end of the arrest 47 heartbeats min^{-1} were noted and with the appearance of blood elements in the vessels they decreased to 36 min^{-1} again. At the time of pre-hatching phase we observed 115 beats min^{-1} and during arresting in this stage the heartbeats decreased to 80 min^{-1}. In the time of hatching 112 heartbeats min^{-1} were stated.

DEVELOPMENT IN THE LARVAL PERIOD

a) The protopterygiolarva

The newly hatched protopterygiolarva of *A. gardneri* is 4.5—5 mm long, that of *A. scheeli* about 5.3 mm long. The yolk is nearly total absorbed in both species and the larvae do eat immediately naupha of the brain-shrimps or

cladocerans. The caudal fin has 9 lepidotrichia. The fin fold is complete on dorsal as well as on the ventral side (Fig. 1). On the third day the number of caudal lepidotrichia increased to 11 and the fin fold at the levels on the future

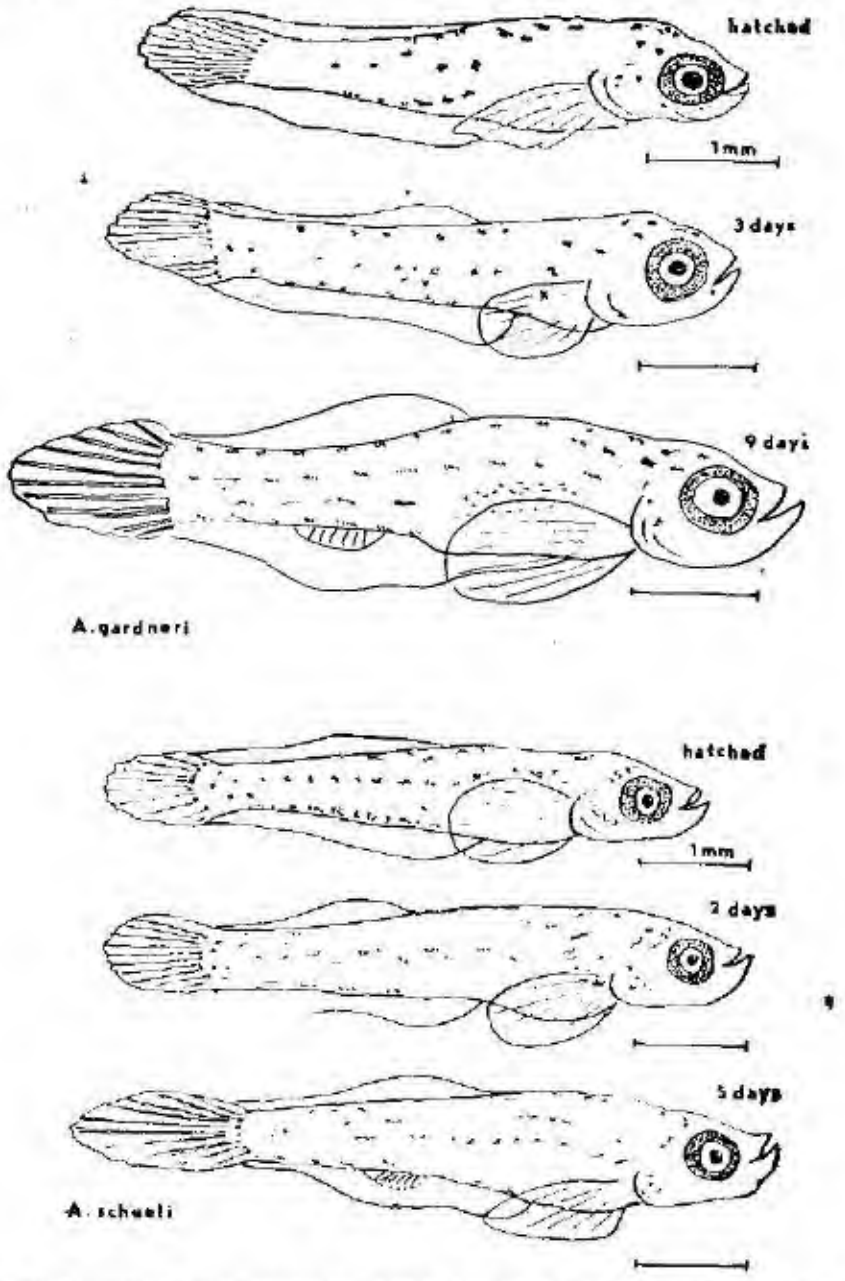

Fig. 1. Development of protopterygiolarvae up to the first stage of pterygiolarva: *A. gardneri* (top) and *A. scheeli* (bottom).

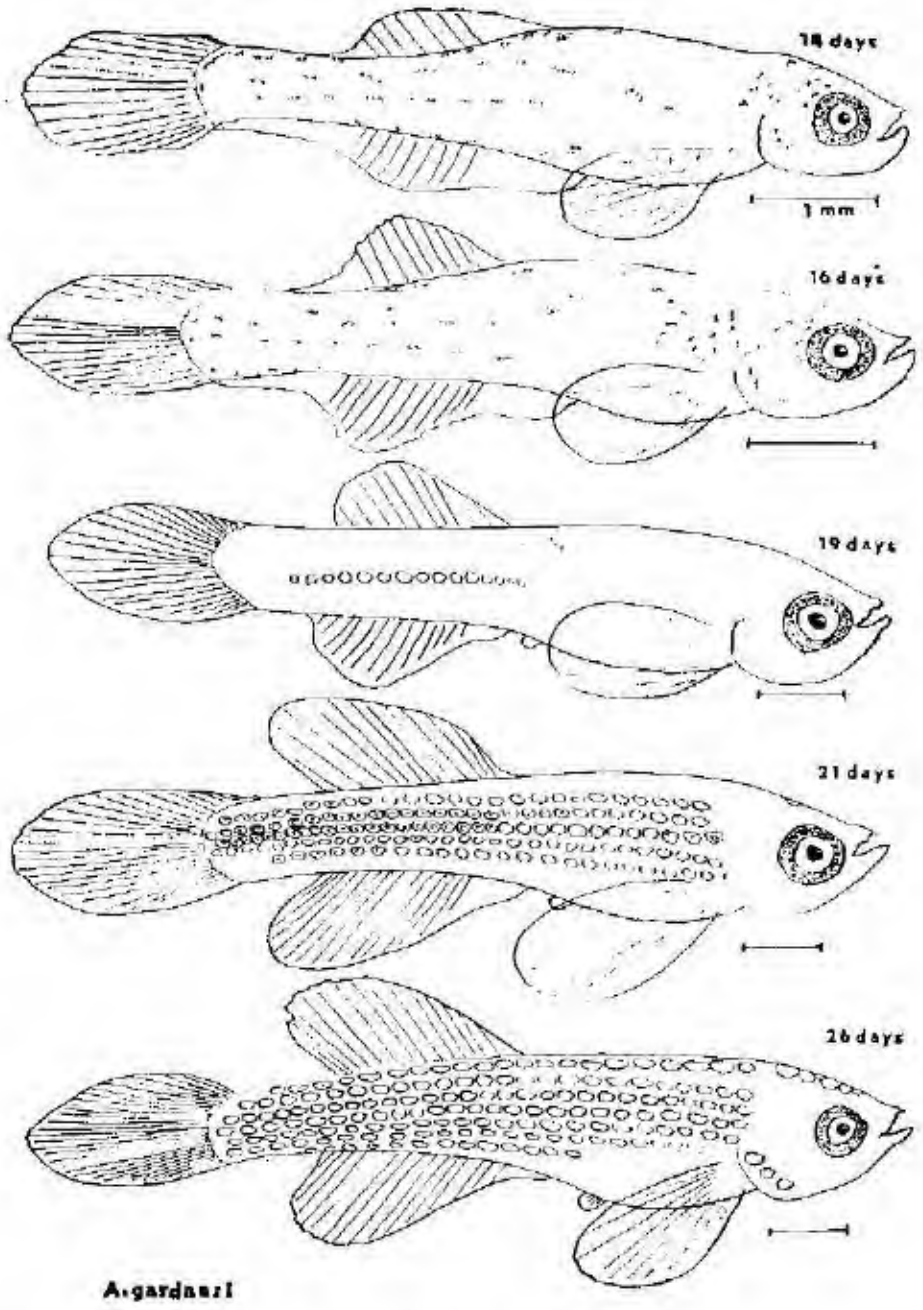

Fig. 2. Development of pterygiolarva of *A. gardneri*.

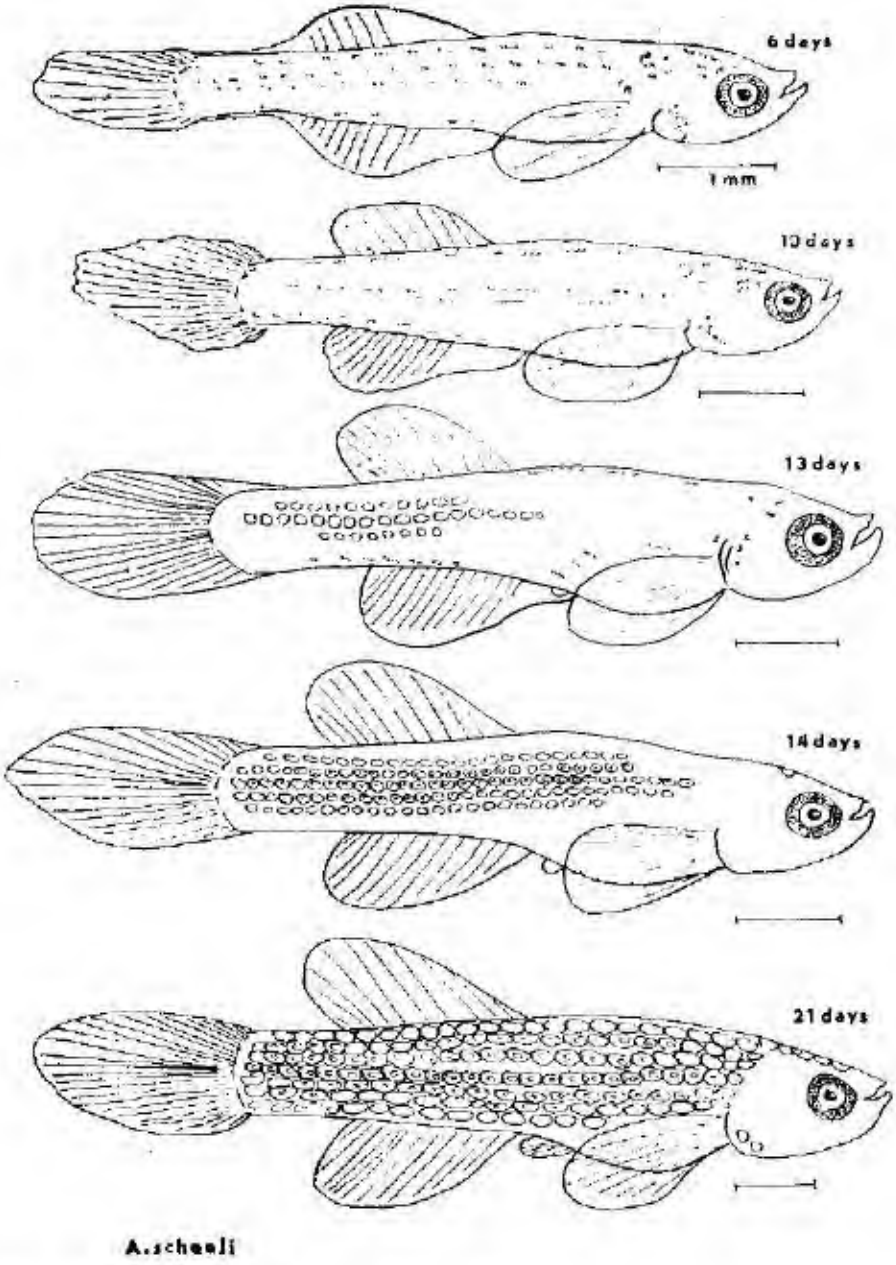

Fig. 3. Development of pterygiolarva of *A. scheeli*.

dorsal and anal fin was more differentiated (Fig. 1). The length of the three days old protopterygiolarva of *A. gardneri* is 5.5 mm, that of *A. scheeli* 6 mm. in average.

Tab. 2. Increasing of the number of lepidotrichia in caudal (C), dorsal (D) and anal (A) fins during the growth of pterygiolarvae

A. gardneri				*A. scheeli*			
C	D	A	age in days	C	D	A	age in days
12	—	6	9	12	—	6	6
14	3	6	11	14	3	6	7
16	7	9	14	20	8	11	10
20	9	11	16	20	11	13	13
24	10	13	19				
24	12	14	20				
28	12	14	21				

b) The pterygiolarva

First lepidotrichia in the fin fold can be distinguished on the future anale at 9 days in *A. gardneri* and 6 days in *A. scheeli*, respectively. The further development and lepidotrichia in caudale, dorsale and anale of both species is given in Tab. 2 and Figs 2 and 3.

The fin fold was gradually absorbed and the fins separate. Very interesting is the late development of pelvic fins. They appear as a simple lobe at 19 days in *A. gardneri* and 12 days in *A. scheeli*. The development of pelvic fins is in retlation to the development of scales. They appear with the first row of scales and their rays appear after the whole body is covered with scales.

The first row of scales appear on the posterior part of the body. First scales are visible on about the level of the oral end of dorsale and the row extends in both directions, but more quickly to the caudal end of the body. The second row develops in the same manner on the dorsal side of the first row, the third row on the ventral side of of the firts row. Three rows of scales are developed in *A. gardneri* in 20 days and in *A. scheeli* in 13 days. Than, again, the fourth row develops on the dorsal side of the second, and the fifth on the ventral side of the third at the age of 21 days in *A. gardneri* and 14 days in *A. scheeli*, respectively. At this time the scale A, coverning the pineal organ on the top of the head, develops. The last rows of scales are the rows 6 and 7, developing above the 4th and beneath the 5th row of scales. With the occurrence of the first scales of the row 6 we can observe two other scales on the head, too. There are the E scales, on the 24 day in *A. gardneri* and 17 day in *A. scheeli*. On the day 28 in *A. gardneri* and 21 in *A. scheeli* 7 rows of scales are full developed and on the head the scales G, D and C are visible. At the same time the first scales on the angulum of the gillcovers develop, too. The length of larvae at this stage is about 12 mm. The pterygiolarval stage ends and the juvenile stage of the fish begins.

DISCUSSION

a) Mortality during the embryonal development

The correlation between water-hardness and mortality of fish eggs was studied in detail by Frank (1973, 1974, 1975). We can compare before all his investigations made on *Roloffia roloffi*, the close relative of the genus *Aphyo-*

semion. In our species, however, the tolerance to the carbonate hardness is apparently higher than in *Roloffia*. In the water of approximately same quality as in our investigations the mortality in *Roloffia* was about 50 % (cf. Fig. 9 in Frank 1974), but in our species the mortality in *A. gardneri* was 15 % and in *A. scheeli* 8 % only.

b) Development in the early embryonic phase

The development up to the stage of late gastrula was shorter (about 10 h) than that of *Fundulus heteroclitus* (about 20 h), as given by Oppenheimer (1937), in spite of a lower temperature in our investigation (19—25 °C against 27 °C). We can observe some delay in the development, so that the early somite embryo stage was reached later in our species (58 h) than that of *F. heteroclitus* (about 30 h). The eggs ob both our species of *Aphyosemion* hatch at about the same time as the eggs of *F. heteroclitus* (in average 8—13 days). If compared with the strongly annual species *Austrofundulus myersi* (cf. Wourms 1972 a), only the early two- and four-cell stages were reached at the comparable time but, the subsequent development was longer in annual *Austrofundulus*. It seems that the time of development of early stage of cleavage eggs is the same or, comparable same in other species of fishes, too (Balon 1956 a, b, 1958, 1959, 1960, 1977, Frank 1956) and just in the later stages of embryonal development speicfic differences occur.

c) Development in the larval period

In both investigated species the yolk was neraly fully absorbed and the larvae do eat almost immediately. This is not the case in all *Aphyosemion* species, on the contrary, most of them hatch with comparatively great yolk sac, which is absorbed in the period of some hours, up to two days in various species (unpublished investigations of the author). Detail knowledge about the development of various fishes is quite scarce and very little is known of the development of Cyprinodontidae. In most fishes the pelvic fins develop in the early stage of pterygiolarva, mostly at the end of the endogenous nutrition (Ahlstrom & Ball 1954, Balon 1956, 1958, 1959, 1977, Balon & Frank 1953, Frank 1956) but, it seems that the late deevlopment of pelvic fins in Cyprinodontidae is obvious (Oppenheimer 1973, Wourms 1972 a). In the genus *Simpsonichthys*, the pelvic fins are absent at all even in adult specimens.

SUMMARY

The development in *A. gardneri* is longer than that of *A. scheeli* under the same conditions. In *A. gardneri* the so called "resting eggs" may develope, which are arrested in the stage of the long somite embryo (diapause II.) and in the pre-hatching stage (diapause III.) again. The phase of the protopterygiolarva lasts 9 days in *A. gardneri* and 6 days in *A. scheeli*, the phase of pterygiolarva lasts 26 days in *A. gardneri* and 21 days in *A. scheeli*. The scalation is of the caudo-oral type and the first scales occur at the age of 19 (*A. gardneri*) and 17 (*A. scheeli*) days. At this time the pelvic fins develop in the form of simple lobes. On the top of the head the scale. A is visible in 21 days in *A. gardneri* and in 14 days in *A. scheeli*. At 24 days (*A. gardneri*) and 17 days (*A. scheeli*) the E scales develop. Scales G, D and C occure at the age of 26 (*A. gardneri*) and 21 (*A. scheeli*) days. At this time of transition to the juvenile

stage the fish have 7 rows of scales and the first scales on the gill covers develop. Only just now the pelvic fins develop the lepidotrichia.

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A CASE STUDY ON THE REPRODUCTIVE CAPACITY OF COMMON CARP, CYPRINUS CARPIO (PISCES: CYPRINIDAE) FROM INDIA

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Abstract. The paper deals with the reproductive capacity of common carp *Cyprinus carpio* Linnaeus which is an important member of the composite fish culture system in India. The total fecundity ranged from 3,127 in a fish measuring 20 mm in total length, 315 g in body weight and 65 g in ovary weight to 298,921 in a fish measuring 550 mm in total length, 2.85 Kg in body weight and 545 g in ovary weight. A straight line relationship was obtained between the fecundity and other body parameters after fitting the straight line equation. The study showed that the fecundity and fish weight relationship was more closely related ($r = 0.9494$) than the fish length ($r = 0.9458$) and ovary weight ($r = 0.7657$).

INTRODUCTION

Composite fish culture is a widely accepted system of fish farming throughout the world which yeilds maximum production in any water body. *Cyprinus carpio* Linnaeus (var. *communis*) is one of the important member of this system alongwit *Catla catla*, *Cirrhinus mrigala*, *Labeo rohita*, *Hypophthalmichthys molitrix* and *Ctenopharyngodon idellus*. The fish is reaerd at Gujartal Fish Farm, where the present study was made by the senior author in 1983.

C. carpio was brought to India in 1957 from Bangkok (Jhingran, 1982) and was distributed all over India for culture by CIFRI. It is voracious omnivorous with fast growth and is prone to artificial feed. Some important contributions to the biology of common carp in India are made by Alikunhi (1966), Alikunhi and Chaudhury (1959), Hora and Pillay (1962) and Parmeswaran et al. (1972). Present communication deals with the fecundity of common carp at Gujartal fish farm, Jaunpur, India and its relationships with different body parameters.

MATERIAL AND METHODS

Twenty six mature specimens of *C. carpio* were selected and all the body measurements were recorded in fresh condition. The ovary of each fisch was dissected and preserved in 5% formalin solution. The fecundity of fish was recorded by gravimetric count method and studied in relation to total length, body weight and ovary weight of the fish. For the total fecundity estimation, 3 random samples of 10 mg each were taken from the anterior, middle and posterior regions of each ovary of each specimen. The number of ova in each sample were counted under a binocular microscope and total number of eggs in each ovary were estimated by the following formula:

$$F = S \times OW/100$$

where F = fecundity, S = average number of eggs obtained from 6 different samples of 100 mg each and OW = total weight of ovary in Mg. The relationship between

fecundity and other body parameters were obtained by plotting the original values as a scattered diagram and after getting a curvilinear pattern, the values were converted into their respective log values and a straight line relationship was obtained by the method of least squares (ie. Log Y = Log a + b log X).

RESULTS

Fecundity and fish length

The relationship between fecundity and fish length is shown in Fig. 1. The number of ova varied from 43,127 for a fish of 250 mm to 298,921 in the fish

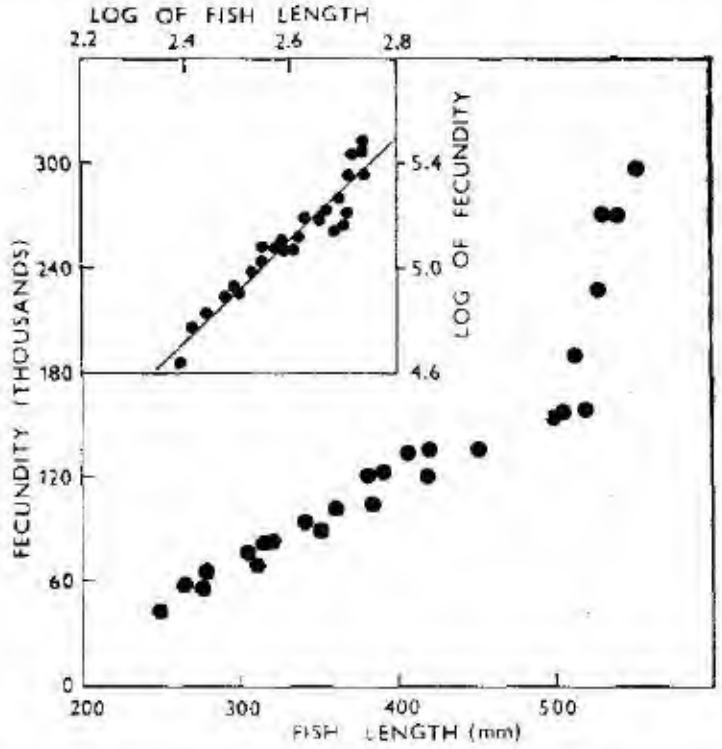

Fig. 1. Relationship between fish length and fecundity in *C. carpio*.

measuring 550 mm. The relationship between fecundity and total length was observed to be as:

Log F = 0.083417 + 1.925 FL (r = 0.9458)

where F = fecundity, FL = fish length and r = correlation coefficient.

Fecundity and fish weight

The relationship between fecundity and fish weight is represented in Fig. 2. Egg production ranged from 43,127 in a fish of 0.315 kg to 298,921 in a fish of 2.85 Kg. The mean values of relative fecundity ranged from 0.68672 to 1.79105 Kg body weight. The fecundity — body weight relationship can be expressed as:

Log F = 3.0289 + 0.68135 FW (r = 0.94946)
where FW = fish weight.

Fecundity and ovary weight

The relationship is expressed in Fig. 3. Egg production ranged from 43,127

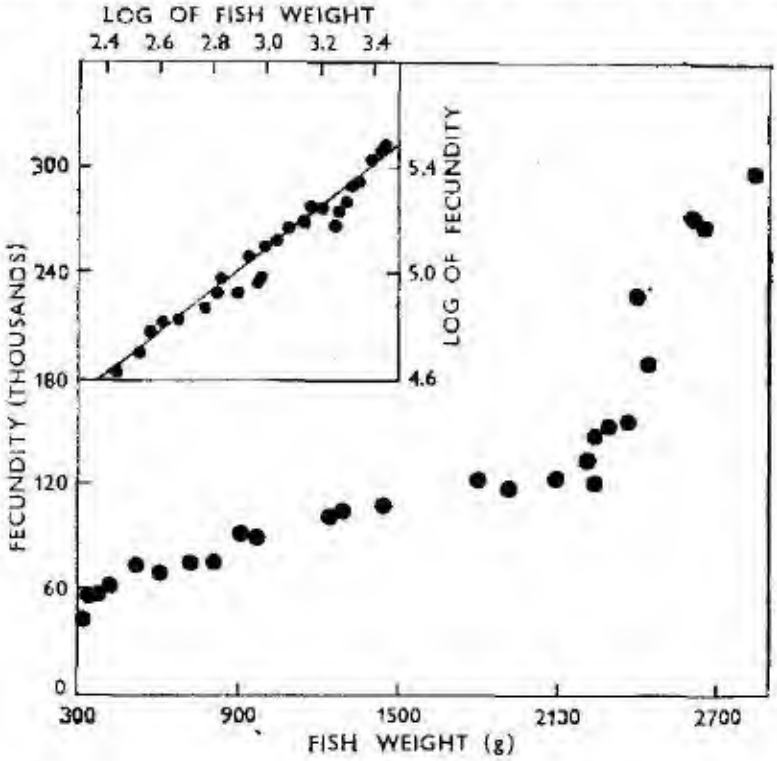

Fig. 2. Relationship between fish weight and fecundity in *C. carpio*.

in an ovary of 85 g to 298,921 in an ovary of 545 g. The fecundity-ovary weight relationship can be expressed as:

Log F = 3.9434 + 0.46697 OW (r = 0.76575)
where OW = ovary weight

Gonado-somatic index

GSI of each fish was calculated and it was found that fish ranging from 300—400 mm in length got the maximum GSI. ie., 24.5 (Fig. 4).

DISCUSSION

Cyprinus carpio attains sexual maturity at different age and size in different parts of the world. In Japan it attains maturity in the second year (Matsui, 1957), in Israel in the first year (Sarig, 1966) and in Malaysia only in 6 months (Buschkiel, 1933). In India the fish attained sexual maturity

within 6 months in the plains (Alikunhi, 1966) but in tarain region of Shiwalik Himalayas, it took 10 months time to become mature (Singh and Singh, 1979). The fish selected for the present study were more than one year old.

The fecundity of fish has already been studied by several workers (Clark, 1934; Khan, 1945; Varghese, 1973; Singh et al., 1982; Dobriyal, 1988). In *C. carpio* the fecundity ranged from 43.127 in a fish measuring 250 mm in total length, 315 g body weight and 65 g ovary weight to 298.921 in a fish

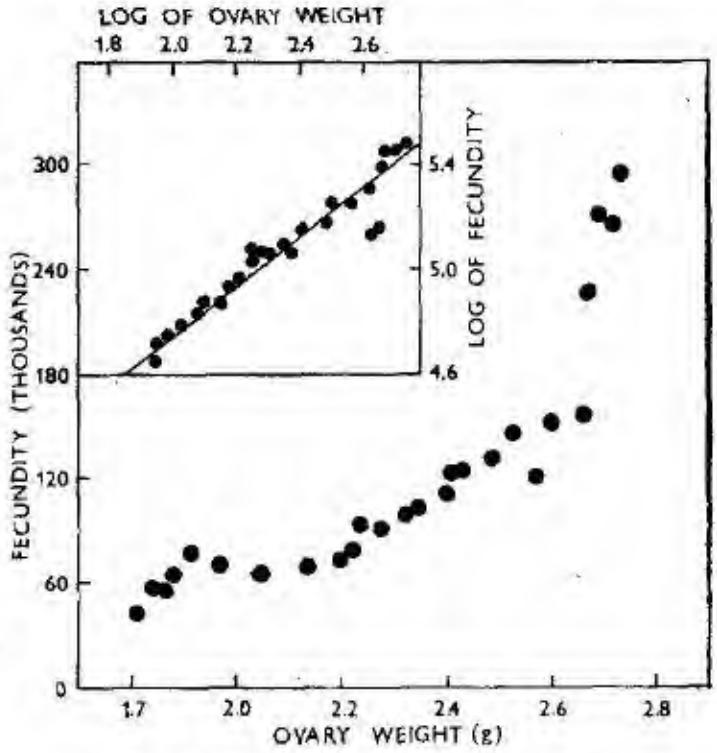

Fig. 3. Relationship between ovary weight and fecundity in *C. carpio*.

measuring 550 mm in total length, 2.85 Kg in weight and 545 g in ovary weight. The relative fecundity calculated for *C. carpio* ranged from 68,672 to 179,105/ Kg body weight. Alikunhi (1966) observed the fecundity of common carp in a range of 437—941/ g body weight which is quite high in comparison to the present observations. Novak and Kostomarov (1937) have stated that mature ova of common carp were of 0.9 to 1.0 mm diameter in Czechoslovakia. The present study (ova diameter 1.0 to 1.5 mm) revealed that under Indian conditions the ova are much larger which supported the idea of Parmeswaran et al. (1972).

In *C. carpio* the fecundity increased with an increase in the body parameters. A curvilinear relationship was observed between the fecundity and other body

parameters which was converted into a straight line after converting the values into their respective log forms. There are several reports on the straight line relationship between fecundity and other body parameters (Bagenal, 1957; Sarojini, 1957; Dobriyal, 1988). However, the curvilinear relationship has also been reported by Varghese (1976).

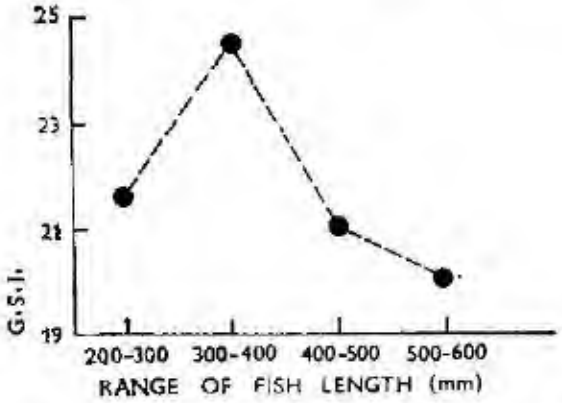

Fig. 4. Gonado-somatic index of mature females at different length groups in *C. carpio*.

The study showed that the fecundity and fish weight relationship was more closely related ($r = 0.9494$) than the fish length ($r = 0.9458$) and ovary weight ($r = 0.7657$).

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FORAMEN MAGNUM AREA IN BIRDS

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Abstract. A review of the foramen magnum area in birds is presented. Overall, data on the foramen magnum area are given for 174 extant species belonging to 42 families of birds. Allometric relationships between the foramen magnum area and the body size and between the foramen magnum area and the brain size are estimated in 6 families of birds and in non-Passeriformes as a whole.

INTRODUCTION

Body elements are generally known to scale interspecifically with the body size (Röhrs 1958, 1961, Gould 1966). This applies also to the nervous system, particularly the brain (Jerison 1973, Szarski 1980, and many others).

In birds, allometric relationships of the brain size to the body size were recently summarized by Mlíkovský (1989 a-c, 1990). However, no such study exists thus far for the foramen magnum area in birds, although Wiedenfeld (1985) established that it is closely correlated with body mass at the interspecific level. This relation was for the first time found in mammals by Radinsky (1967) who stressed its importance for comparative neurology by pointing out that the foramen magnum area is highly correlated with, though larger than, cross-sectional area of medulla, approximately at the point where medulla oblongata transgrades into medulla spinalis. In the present paper, a first review of the foramen magnum area in birds will be presented, with special respect to the relation of the foramen magnum area to the body size and to the brain size. Anatomical nomenclature follows Baumel et al. (1979) throughout the present paper.

It should also be noted here, that foramen magnum is an important osteological feature of the occipital part of the avian skull. This region received remarkably less attention from morphologists thus far. Important exceptions are the Duijm's (1951) discussion of the inclination of foramen magnum in relation to the skull basis and the Goedbloed's (1958) comparative study of the condylus occipitalis in birds.

I thank R. Piechocki (Halle/Saale), G. Mauersberger and B. Stephan (Berlin) and J. Hanzák and I. Heráň (Praha) for permissions to study avian skulls under their care.

MATERIAL

All the skeletal material investigated in this study is from the collections of the Department of Zoology of the National Museum in Praha, Czechoslovakia; the Institute of Zoology of the Martin Luther University in Halle (Saale), East Germany;

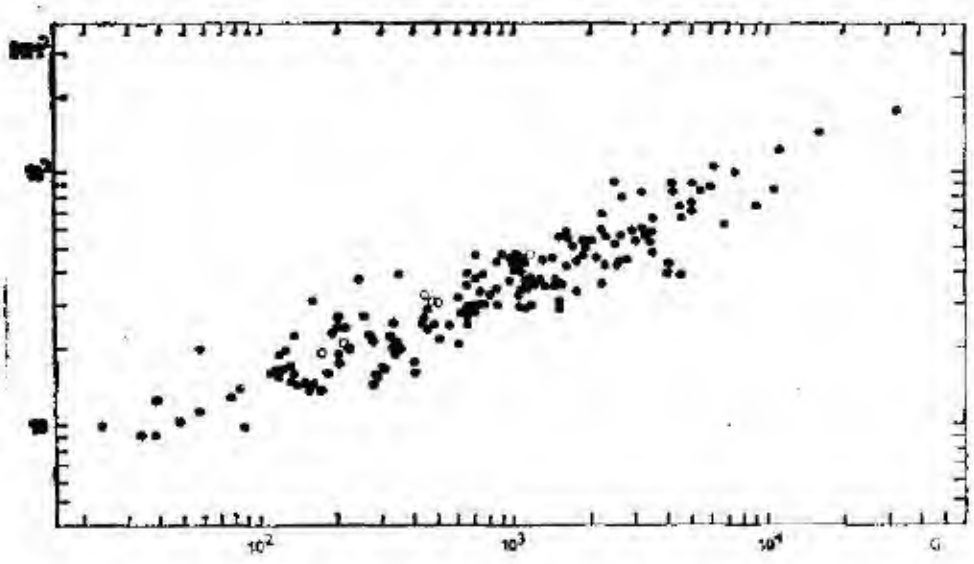

Fig. 1. Relationship between the foramen magnum area (Y axis) and the body mass (X axis) in birds. • = non-Passeriformes, o = Passeriformes. See Table 1 for exact data.

and the Museum of Natural History of the Humboldt University in Berlin, East Germany. A complete list of measurements is given by Mlíkovský (1985).

Measurements were made on 523 skulls from 166 extant species belonging to 41 different families of birds. These measurements were supplemented by the data published by Stephan (1979) on the foramen magnum in penguins. The aggregate data contains estimates of foramen magnum area in 554 skulls from 174 species belonging to 42 families of birds.

METHODS

Maximum dorsoventral and transversal diameters of foramina magna were measured with a sliding caliper to an accuracy of 0.1 mm. Using these measures, foramen magnum area was calculated according to the formula for the area of ellipses (Bartsch 1981). For methods of estimating body size and brain size see Mlíkovský (1989 a). Note that data on brain size given in the present paper may differ from those given by Mlíkovský (1989 a—c, 1990). This is because only those brain size estimates were used here when foramen magnum area was estimated for the same skull. The few exceptions are mentioned below.

Foramen magnum area was expressed as a function of body size and brain size by allometric equations $F = b . S^a$ and $F = b . E^a$, respectively, where F is foramen magnum area (mm^2), E is brain size (volume; cm^3), S is body size (mass; g), a is allometric exponent or slope and b is intercept. The allometric equation is linear after logarithmic tarnsformation. The coefficients a and b appearing in allometric equations were determined by the reduced major-axis analysis (see Seim and Saether 1983).

Correlations between variables were tested for significance using Olkin and Pratt's (1958) modification of the Bravais' correlation coefficient (r^*). Statistical comparisons were calculated according to standard formulas (Sachs 1974). In the following, a 5% probability level is taken as significant for Type I errors (cf. Sachs 1974: 95).

Table 1. Foramen magnum area in birds. n = number of measured skulls (figures in parentheses are for brain size estimates, if different), S = body size (g), E = brain size (cm^3), F = foramen magnum area (mm^2). All measurements are by the author, except of those of the foramen magnum area in the Sphenisciae which were taken from Stephan (1979). The sequence of families follows Storer (1971), species limits are after Wolters (1975 – 1982)

Taxon	n	S	E	F
Tinamidae				
Crypturellus soui	1		1.9	16.5
Crypturellus tataupa	1		1.1	11.7
Podicipedidae				
Podiceps grisegena	6	720	3.05	29.8
Podiceps cristatus	9	1 070	3.8	34.0
Podiceps auritus	1	480	2.4	25.0
Podiceps nigricollis	1	330	1.7	19.2
Tachybaptes ruficollis	13	200	1.6	18.8
Spheniscidae				
Aptenodytes forsteri	4	32 000	44.3	175.7
Aptenodytes patagonicus	3(1)	16 000	28.5	142.8
Eudyptes chrysolophus	1	4 200	13.0	84.6
Eudyptes crestatus	3(1)	2 500	13.5	91.8
Pygoscelis adeliae	2	5 000	17.5	90.6
Pygoscelis papua	8(3)	6 200	18.5	107.3
Spheniscus humboldti	2	4 200	17.5	90.6
Spheniscus demersus	8(5)	2 700	13.7	81.9
Procellariidae				
Diomedea sp.	1		27.5	113.0
Fulmarus glacialis	1	700	7.0	46.9
Sulidae				
Sula bassana	3	3 200	19.5	82.8
Phalacrocoracidae				
Phalacrocorax pygmaeus	2	700	4.2	27.8
Phalacrocorax carbo	14	2 100	10.8	46.0
Anseridae				
Anseranas semipalmata[1]	1	2 200	9.5	69.1
Cygnus cygnus	1	9 000	16.0	74.2
Cygnus olor	6	10 500	14.9	86.2
Coscoroba coscoroba	2	3 500	9.25	58.1
Anser cygnoides	1	3 500	12.0	65.7
Anser fabalis	3	2 800	12.0	58.8
Anser erythropus	2	1 850	6.8	46.8
Anser anser	3	3 350	11.2	53.3
Branta leucopsis	1	1 760	8.0	44.8
Branta bernicla	2	1 400	6.1	46.6
Branta ruficollis	2	1 280	5.1	35.5

cont.

Taxon	n	S	E	F
Cereopsis novaehollandiae	1	3 500	9.0	48.4
Chloephaga picta	1	2 580	6.5	43.6
Alopochen aegyptiacus	3	2 300	7.1	56.7
Tadorna tadorna	2	1 100	5.3	36.9
Tadorna ferruginea	2	1 250	4.8	37.4
Anas penelope	1	740	4.4	33.7
Anas strepera	2	650	3.4	28.8
Anas crecca	2	325	2.7	21.9
Anas querquedula	3	330	2.5	20.1
Anas luzonica	2	950	5.05	37.4
Anas platyrhynchos	3	1 100	5.9	44.7
Anas clypeata	2	610	3.45	28.1
Netta rufina	5	1 160	4.9	38.4
Aythya ferina	2	850	5.4	29.4
Aythya collaris	1	700	4.7	37.9
Aythya marila	1	1 000	5.3	45.3
Somateria mollissima	4	2 000	8.0	54.2
Clangula hyemalis	1	650	5.8	40.1
Melanitta nigra	8	980	5.9	43.4
Melanitta fusca	2	1 500	7.7	56.4
Bucephala clangula	1	900	6.0	47.2
Mergus albellus	1	650	4.0	35.6
Mergus serrator	2	1 050	5.1	33.6
Mergus merganser	2	1 300	6.7	45.4
Phoenicopteridae				
Phoenicopterus ruber	2	3 000	10.8	54.1
Ardeidae				
Botaurus stellaris	3	1 150	6.5	29.4
Ixobrychus minutus	1	170	1.6	13.8
Nycticorax nycticorax	2	650	5.15	24.9
Ardeola ibis	2	340	3.7	20.8
Ardeola ralloides	2	180	2.2	16.1
Ardea cinerea	8	1 500	8.25	31.1
Egretta garzetta	2	500	3.35	22.2
Casmerodius albus	1	1 100	6.0	29.2
Threskiornithidae				
Plegadis falcinellus	2	690	4.45	28.6
Platalea leucorodia	2	1 700	10.75	51.2
Ciconiidae				
Ciconia nigra	4	2 700	11.9	45.3
Ciconia abdimii[2]	1(2)	1 450	8.25	37.2
Ciconia episcopus	1	2 250	10.3	42.8
Ciconia ciconia	14	3 300	15.4	55.9
Cathartidae				
Coragyps atratus	2	1 900	10.0	49.5
Vultur gryphus	1	11 000	31.5	122.5
Sarcoramphus papa	1	4 500	21.0	72.3

cont.

Taxon	n	S	E	F
Accipitridae				
Gyps fulvus	1	7 500	26.5	100.3
Gypaetus barbatus	2	6 000	24.25	88.7
Haliaeetus albicilla	41	5 000	19.0	75.9
Haliaeetus leucocephalus	2	5 000	18.25	70.0
Milvus milvus	3	1 100	8.2	45.4
Milvus migrans	8	850	7.25	45.0
Pernis apivorus	3	750	7.1	39.6
Accipiter gentilis	10	1 000	7.95	46.0
Accipiter nisus	7	200	2.9	24.5
Buteo lagopus	5	1 000	9.0	45.7
Buteo buteo	12	1 000	8.4	46.2
Aquila chrysaetus	3	4 500	17.3	66.7
Aquila clanga	1	2 200	11.5	58.4
Aquila pomarina	2	1 600	10.75	55.1
Circus aeruginosus	5	600	5.8	31.9
Circus cyaneus	8	450	4.6	29.2
Pandion haliaetus	1	1 600	9.9	56.7
Falconidae				
Falco peregrinus	1	800	6.2	32.6
Falco columbarius	3	190	2.8	23.3
Falco tinnunculus	3	200	4.0	26.4
Falco vespertinus	1	160	2.7	31.3
Falco subbuteo	1	240	3.6	37.9
Cracidae				
Crax alector	1		7.0	44.2
Phasianidae				
Tetrastes bonasia	1	400	1.7	17.7
Lyrurus tetrix	1	1 050	3.7	29.2
Tetrao urogallus	2	4 500	5.6	39.0
Pavo cristatus	1	4 000	5.0	40.7
Chrysolophus pictus	1	600	2.7	21.2
Phasianus colchicus	6	1 500	3.7	29.1
Crossoptilon auritus	1	1 750	5.9	34.2
Gallus gallus (wild)	1	850	3.1	35.2
Perdix perdix	1	400	1.75	15.9
Coturnix coturnix	1	90	0.7	9.2
Meleagris gallopavo (wild)	1	4 000	6.0	43.6
Rallidae				
Porzana porzana	1	80	1.0	12.3
Gallinula chloropus	1	280	1.9	15.5
Fulica americana	1	430	2.9	25.4
Fulica atra	4	650	3.4	27.4
Heliornithidae				
Heliornis fulica	1	135	1.4	22.5

cont.

Taxon	n	S	E	F
Gruidae				
Grus grus	3	5 500	18.5	83.8
Anthropoides virgo	5	2 500	9.4	42.9
Balearica pavonina	4	3 250	13.0	58.6
Psophiidae				
Psophia crepitans	1	1 000	5.8	41.1
Otididae				
Otis tarda	17	6 600	10.6	82.0
Haematopodidae				
Haematopus ostralegus	1	550	4.0	24.8
Recurvirostridae				
Recurvirostra avocetta	1	340	1.9	20.5
Charadriidae				
Vanellus vanellus	1	200	2.2	20.5
Scolopacidae				
Scolopax rusticola	4	330	2.4	25.2
Philomachus pugnax	1	155	1.4	13.8
Gallinago gallinago	2	130	1.35	17.0
Lymnocryptes minimus	1	60	0.9	19.6
Numenius arquata	1	760	4.4	29.4
Actitis hypoleucos	1	50	0.7	9.9
Laridae				
Larus canus	2	450	3.7	24.0
Larus ridibundus	1	300	2.8	16.7
Sterna hirundo	1	135	1.7	15.7
Alcidae				
Cepphus grylle	2	430	3.05	26.0
Uria aalge	1	1 050	5.4	40.9
Gaviidae				
Gavia stellata	1	1 800	6.0	42.8
Gavia arctica	10	2 500	7.5	52.3
Columbidae				
Goura cristata	1	2 200	5.7	35.8
Zenaidura macroura	1	120	1.1	15.5
Streptopelia turtur	1	125	1.4	16.3
Streptopelia decaocto	1	275	1.4	14.5

cont.

Taxon	n	S	E	F
Psittacidae				
Forpus passerinus	1	25	1.0	9.5
Agapornis pullarius	1		1.4	10.7
Anodorhynchus hyacinthinus	1		24.5	59.7
Psittacus erithacus	1	350	8.0	30.6
Psittacula alexandri	3	125	3.6	19.5
Trichoglossus haematodus	4	150	2.4	14.6
Platycercus eximius	1	110	2.5	16.0
Platycercus elegans	1	135	3.7	14.7
Cuculidae				
Clamator glandarius	1	135	1.7	14.3
Cuculus canorus[2]	1(9)	120	1.6	15.6
Strigidae				
Tyto alba	1	275	5.0	21.4
Asio otus	6	270	6.0	21.8
Strix aluco	10	500	9.0	30.3
Bubo poensis	1	1 450	9.0	36.1
Bubo virginianus	1	1 500	18.5	47.1
Bubo bubo	22	2 600	17.4	56.9
Bubo capensis	1	1 200	11.5	36.8
Nyctea scandiaca	1	1 900	18.0	53.4
Athene noctua	1	120	4.5	18.7
Ninox scutulata	1	220	3.1	20.2
Apodidae				
Apus apus	1	40	0.8	12.2
Alcedinidae				
Alcedo atthis	1	40	0.8	8.7
Coraciidae				
Coracias garrulus	1	160	1.8	14.2
Upupidae				
Upupa epops	1	60	1.3	11.0
Ramphastidae				
Ramphastos tucanus	1		5.0	24.5
Picidae				
Dendrocopos major	3	85	2.4	13.7
Picus viridis	1	200	3.9	24.7
Dryocopus martius	1	250	8.9	26.7
Jynx torquilla	1	35	0.8	8.3

cont.

Taxon	n	S	E	F
Eurylaimidae				
Cymbirhynchus macrorhynchus	1		1.4	14.8
Cotingidae				
Pyroderus scutatus	2		4.45	23.3
Tyrannidae				
Colonia colonus	1		1.3	12.0
Corvidae				
Corvus corax	41	1 150	14.5	47.7
Corvus americanus	1		9.0	23.7
Corvus corone	3	470	8.7	31.2
Corvus frugilegus	2	440	7.5	33.1
Garrulus glandarius	2	170	3.95	19.4
Pica pica	1	210	5.2	21.1

[1]) Excluded from the calculations for the family Anseridae.
[2]) Brain size and foramen magnum area estimated on different skulls.

RESULTS

The data were sufficient for calculation of regression equations in 6 families of birds and in non-Passeriformes as a whole (Figure 1, Table 1). The results are presented below.

In Spheniscidae, foramen magnum area is positively correlated with both body size ($r^* = 0.976$, $p < 0.001$) and brain size ($r^* = 0.975$, $p < 0.001$). Their allometric relations are $F = 6.792\ S^{0.313\pm0.0328}$ and $F = 16.232\ E^{0.631\pm0.0651}$, respectively ($n = 8$). When the effect of body size is removed by the partial correlation analysis, foramen magnum area and brain size ceaze to be correlated ($r^*_{FE.S} = 0.497$, n.s.).

In Ardeidae, foramen magnum area is positively correlated with both body size ($r^* = 0.988$, $p < 0.001$) and brain size ($r^* = 0.990$, $p < 0.001$). Their allometric relations are $F = 2.472\ S^{0.353\pm0.0251}$ and $F = 10.852\ E^{0.525\pm0.0332}$, respectively ($n = 8$). Foramen magnum area and brain size are positively correlated even when the effect of the body size is removed ($r^*_{FE.S} = 0.794$, $p < 0.05$).

In Anseridae, foramen magnum area is positively correlated with both body size ($r^* = 0.885$, $p < 0.001$) and brain size ($r^* = 0.943$, $p < 0.001$). Their allometric relations are $F = 2.443\ S^{0.395\pm0.0329}$ and $F = 12.449\ E^{0.675\pm0.0427}$, respectively ($n = 34$). Foramen magnum area and brain size are positively correlated even when the effect of the body size is removed ($r^*_{FE.S} = 0.704$, $p < 0.001$).

In Accipitridae, foramen magnum area is positively correlated with both body size ($r^* = 0.980$, $p < 0.001$) and brain size ($r^* = 0.984$, $p < 0.001$). Their allometric relations are $F = 3.266\ S^{0.375\pm0.0189}$ and $F = 11.674\ E^{0.642\pm0.0308}$, respectively ($n = 17$). Foramen magnum area and brain size are marginally positively correlated even when effect of the body size is removed ($r^*_{FE.S} = 0.468$, $p < 0.1$).

In Phasianidae, foramen magnum area is positively correlated with both body size ($r^* = 0.958$, $p < 0.001$) and brain size ($r^* = 0.969$, $p < 0.001$). Their allometric relations are $F = 1.585\ S^{0.404\pm0.0411}$ and $F = 11.528\ E^{0.728\pm0.0638}$, respectively ($n = 11$). The correlation between foramen magnum area and brain size approaches

significance even when effect of the body size is removed ($r^*_{FE.S} = 0.622$, $p < 0.1$).

In Strigidae, foramen magnum area is positively correlated with both body size ($r^* = 0.977$, $p < 0.001$) and brain size ($r^* = 0.966$, $p < 0.001$). Their allometric relations are $F = 2.523\ S^{0.391 \pm 0.0317}$ and $F = 7.577\ E^{0.661 \pm 0.0653}$, respectively ($n = 10$). Foramen magnum area and brain size are positively correlated even when effect of the body size is removed ($r^*_{FE.S} = 0.784$, $p < 0.05$).

In non-Passeriformes as a whole, foramen magnum area is positively correlated with both body size ($r^* = 0.932$, $p < 0.001$) and brain size ($r^* = 0.954$, $p < 0.001$). Their allometric relations are $F = 1.799\ S^{0.439 \pm 0.0128}$ and $F = 11.601\ E^{0.619 \pm 0.0654}$, respectively ($n = 159$). Foramen magnum area and brain size are positively correlated even when effect of the body size is removed ($r^*_{FE.S} = 0.811$, $p < 0.001$).

DISCUSSION

As expected, foramen magnum area was found to be correlated both with body size (see also Wiedenfeld 1985) and with brain size, which itself is known to be closely related to body size in birds (Mlíkovský 1989a-c, 1990). Because the relation between foramen magnum area and brain size could have been caused by common dependence on the body size, I removed its effect using partial correlation analysis. The results showed that even after this removal, foramen magnum area and brain size are positively correlated. The only exception found was the Spheniscidae (penguins), but I consider this an artifact, because in this family foramen magnum area and brain size were measured on different skulls, which fact may well have obscured the subtle partial correlation between foramen magnum area and brain size in this family. This finding means that higher encephalized birds possess also relatively larger foramen magnum and, hence, relatively more massive medulla than less encephalized birds.

Another point of interest was whether the correlations between the three studied variables are equal, or differ from each other. Comparisons (performed for non-Passeriformes as a whole) revealed that the brain size is more closely correlated with the body size than the foramen magnum area ($z = 18.011$, $p < 0.001$), but no such difference was found between r^*_{FE} and r^*_{ES} ($z = 1.827$, n.s.), which indicates that foramen magnum area is equally well correlated with body size as with brain size. Not surprizingly, $r^*_{FE.S}$ is significantly lower than r^*_{FE} ($z = 6.613$, $p < 0.001$) which reflects the removed effect of the body size in $r^*_{FE.S}$. After this removal, brain size explains approximately 66 % of the observed variability (the value was 91 % before this removal). Taken together, body size and brain size explain 95 % of the observed variability of the foramen magnum area in birds.

SUMMARY

(1) Data on the foramen magnum area in 174 extant species belonging to 42 different families of birds, and the relations of the foramen magnum area to the body size and the brain size in 6 families and in non-Passeriformes as a whole were presented.

(2) Foramen magnum area was found to be closely correlated both with the body size and with the brain size; the degree of correlation was similar in both cases.

(3) Foramen magnum area was found to be less closely correlated with the body size than the brain size.

(4) Positive correlation between the foramen magnum area and the brain size was found to hold even after the effect of the body size is removed. It means that higher encephalized birds possess a relatively more massive medulla than less encephalized ones.

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VENTROLATERAL THORACIC REGION AND THORACICO-ABDOMINAL JUNCTION OF SOME HELOTREPHIDAE (HETEROPTERA, NEPOMORPHA)

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Abstract. External anatomy of the ventrolateral thoracic region and base of the abdomen in three helotrephid species (*Helotrephes semiglobosus* Stål — Helotrephinae, Helotrephini; *Distotrephes stysi* Polhemus — H., Limnotrephini; *Trephotomas compactus* Papáček, Štys & Tonner — Trephotomasinae) is described, illustrated, and compared with other Nepomorpha, particularly their aquatic groups. The helotrephid models share several synapomorphies with the Pleidae, the most striking being (a) an overlap or contact of the ventral mesepimeral lobe over the propleuron, and (b) the presence of a wing-anchoring knob on the metepimeron. Some new characters unique for helotrephids have been ascertained, viz. (a) fixation of the hemelytron by the hind margin of the cephalonotum, and (b) a large discolopodial scolopophorous organ of the first abdominal segment, with its own chamber. The presence and position of stridulatory mechanisms are discussed. Synapomorphies of the Pleidae & Helotrephidae are liested.

INTRODUCTION

The riparial and aquatic suborder Nepomorpha is often used as a model group of true bugs for various kinds of ecological, physiological and morphological studies. Special attention has been paid to the study of the morphology of its ventrolateral thoracic region and base of the abdomen. The results of studies of these body regions have been recently summarized by Papáček (1987) on the occasion of his investigation of *Plea minutissima* (Leach), a representative of a probable helotrephid sister group, the Pleidae.

The reason for attention that is paid particularly to these body regions is that they are functionally important for respiration. Their anatomy is strongly affected in the aquatic Heteroptera by the method of acquiring and maintaining of the air bubble external to the body and by the circulation of air within this bubble. Various characters of these body regions are commonly used for interpretation of the phylogeny of aquatic bugs. However ,the structure of the pleural region exhibits sometimes interspecific differences, and it is also affected by pterygopolymorphism. This suggests that some of the modifications of the lateral thoracic region represent relatively recent functional adaptations (Parsons, 1974).

The Helotrephidae are a relatively small family of aquatic nepomorphan Heteroptera distributed in the tropics and subtropics of Africa, Asia and Central and South America; its species inhabit a wide range of aquatic habitats, from stagnant to rapidly flowing water bodies, and at least some species

survive the drying-up of their habitats by aestivation (Papáček, Štys & Tonner, 1989). The family differs from the other Nepomorpha especially by (1) a strikingly coleopteriform body shape (less marked in the Idiocorinae), (2) presence of cephalonotum, (3) tendency to the reduction of antennae, and (4) unique modifications of the ovipositor. Cladogenetically, the family is usually interpreted as a sister group of the Pleidae (see a review of opinions by Papáček, Štys & Tonner (1988), review of classification by Štys & Jansson (1988), and a partial modification of that classification by Polhemus (1990).

Almost all papers concerning helotrephids are taxonomically orientated, and the Helotrephidae are the only aquatic heteropteran family for which no comparative data on thoracic anatomy are available. For instance, China (1935) correctly characterized the shape and structure of the so-called "propleural plate" in different taxa as seen in strictly lateral view of the propleuron regardless of what anatomical structure is actually involved. We confirm the correctness of China's observations of the shapes, but we have to disregard them in considering the propleuron as a whole, not just as a sclerite that is seen distorted at a convenient and easily defined angle of observation.

In the present paper we describe the pleural regions of the thorax, and the thoracico-abdominal junction in three model species of the Helotrephidae, and compare the architecture of these regions with other nepomorphans, with particular attention to the aquaic families, especially the Pleidae. The respiratory significance of the structures concerned is only marginally noticed. We attempt in particular (1) to homologize the individual structures, and (2) to identify characters important for the assesment of relationship. Only the species of subfamilies Trephotomasinae and Helotrephinae (Helotrephini and Limnotrephini) have been studied; investigation of the subfamilies Neotrephinae and Idiocorinae is reserved for a later opportunity.

MATERIAL AND METHODS

Material examined. The adults of *Helotrephes semiglobosus* Stål, 1859 recorded as *H. lundbladi* China, 1930 by Papáček, Štys & Tonner (1988) — synonymy fide Polhemus (1990); Helotrephinae: Helotrephini), *Distotrephes stysi* Polhemus, 1990 (H.: Limnotrephini) and *Trephotomas compactus* Papáček, Štys & Tonner, 1988 (Trephotomasinae), all from N. Vietnam: Tam Dao, were studied in detail*); larvae of the first and last species were also available.

Methods. The material was preserved in 70% ethanol, some specimens in Bouin's fixative. The preserved specimens were dissected in 96% ethanol under a stereoscopic microscope. Soft tissues were hand-removed using watchmaker forceps, since clearing in lactic acid (or similarly acting macerating agents) tended to soften and distort the skeleton. The transverse or parasagital sections were made by hand, using a sharp razor blade. Separated parts of the skeleton were mounted in Euparal for microscopic examination. For SEM examination the specimens were lyophilized in a Leybold-Heraeus apparatus, coated with a gold-palladium mixture in a Pollaron apparatus, and studied and photographed under a Tesla Stereoscan BS-...

Terminology. The morphological terminology used here is partly summarized in Fig. 1, and derived mainly from Papáček (1987), Parsons (1967 1974, 1976) and Snodgrass (1927).

*) *Distotrephes stysi* Polhemus, 1990 will have been described when the present paper will be published. In the same paper by Polhemus (1990) also the synonymy *Helotrephes semiglobosus* Stål = *H. lundbladi* China is proposed, and the subfamily Helotrephinae is subdivided into Helotrephini and a new tribe Limno-

trephini (comprising *Limnotrephes*, *Paralimnotrephes*, *Idiotrephes*, *Tiphotrephes*, *Distotrephes* Polhemus, 1990, and *Mixotrephes* Papáček, Štys & Tonner, 1989).

OBSERVATIONS AND DISCUSSION

General notes

Development of te cephalonotum as well as the coleopteroid character of forewings linked with a reduction of their distal portions affect the architecture of the thoracic pleuron in helotrephids which is, moreover, usually also modified by reduction of the hindwings prevailing in the family (Papáček, Štys & Tonner, 1989). We have studied specimens of all the 3 species with micropterous, vestigial hindwings; the situation in *H. semiglobosus* was also compared with two specimens whose hindwings were not reduced.

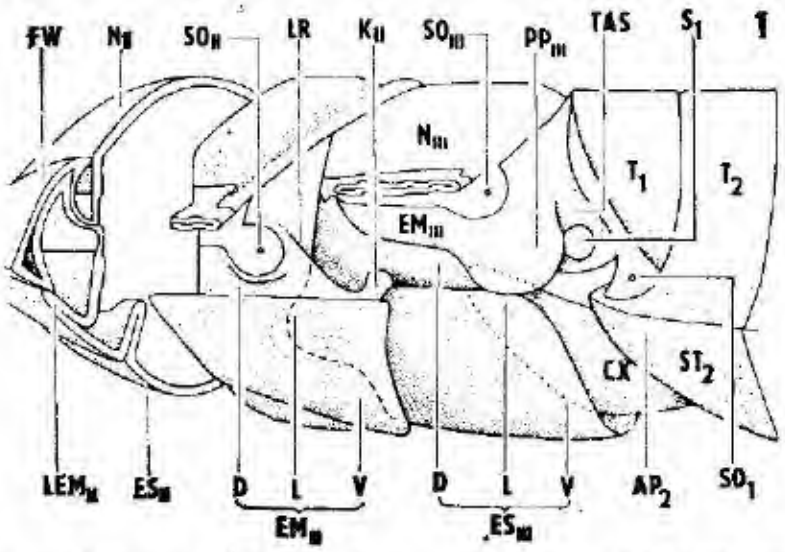


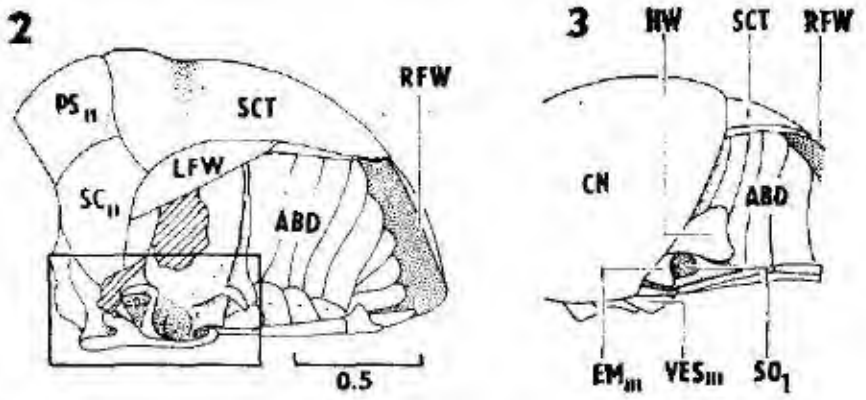
Fig. 1. Model situation of the pterothorax and first two abdominal segments of nepomorphan bugs as illustrated by Parsons (1976, Fig. 14 A) — modified. Diagramatic lateral view. Mesothorax cut transversely, wings cut off. Heavy broken line indicates the position of lateral intersegmental boundary.

Cephalonotum of *H. semiglobosus* is relatively short in terms of the Helotrephidae: its hind margin does not medially reach half the length of the body. Forewings in specimens with reduced hindwings are near their anal margin (a) fused by their dorsal surface with the cephalonotum which covers their whole basal (axillary) region, and (b) by their ventral surface fused with the lateral notalal area of the pterothorax (see Figs. 2,6 — hatched areas). Fusion do not occur in "macropterous" specimens. In *D. stysi* the cephalonotum reaches nearly half the body length and covers the basal parts of forewings up to half the length of the clavulus. The cephalonotum of *T. compactus* is very elongate, reaching 2/3 of total body length, and covers laterally all the pterothorax (Pl. I, Fig. 4)*, extending up to the base of the abdomen. The forewings

* The plates I and II will be found at the end of this issue.

of the 3 species are firmly and more or less immovably attached to the body.

Lateral areas of the pterothoracic pleuron (formed by dorsal parts of the mesepimeron, metepisternum, and metepimeron) are shorter relative to the body length and height than in other nepomorphan Heteroptera (excepting the Pleidae). There are two striking invaginations, viz a "chamber of mesothoracic scolophorous organ" and an "air chamber of the metathoracic spiracle". The pleurally situated axillary region of hindwing is partly to entirely homogenously sclerotized excepting *H. semiglobosus* with non-reduced hindwings.



Figs. 2, 3. 2 — *Helotrephes semiglobosus* — pterothorax and abdomen. Lateral view; cephalonotum, legs and left forewing removed. Rectangle indicates the body region studied. 3 — *Trephotomas compactus* — posterior part of cephalonotum and basal part of abdomen. Lateral view; legs and left forewing removed.

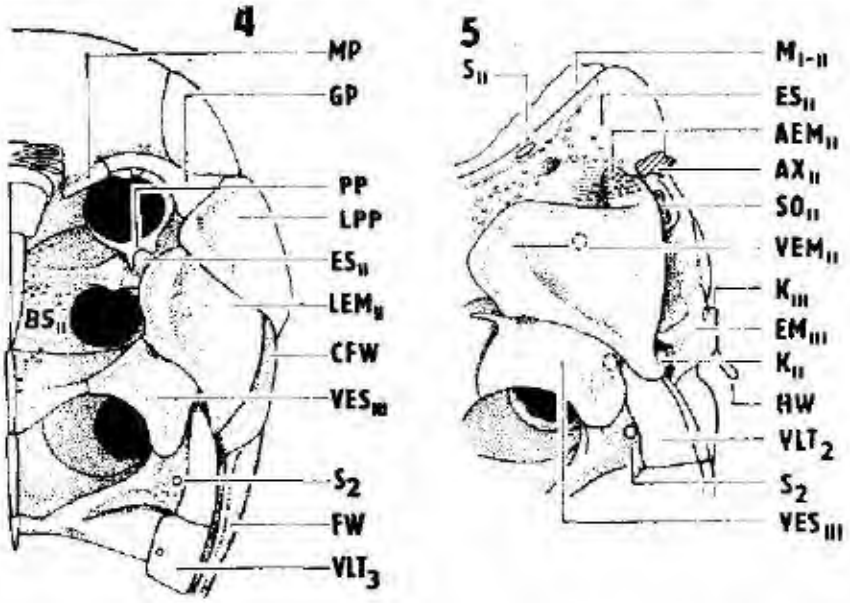
Ventrally situated parts of the pterothoracic pleuron (formed largely by ventral and lateral lobes of the mesepimeron and metepisternum) are distinctly subdivided into sclerites and with a distinct, superficially resembling a single sclerite, and its compactness is reminiscent of the situation in some aquatic beetles.

Propleuron

Popov (1971), who relied upon Matsuda's (1962, 1970) opinion on the homology of pleural sclerites, thought that the nepomorphan propleuron is formed by the epimeron only. However, Larsén (1945 a, b), Papáček (1987), Parsons (1987) and Rieger (1976) explain this region as being formed by both the episternum and epimeron fused to various extents, the epimeron mostly extending caudad as a conspicuous lobe being the main constituent. Parsons (1967) suggested that the degree of fusion of the procpisternum with the procpimeron depends on feeding strategy in the group (linked with the degree of mobility of the procoxa), and, pragmatically, used the criterion of the degree of development of the coxal cleft for assessing propleural architecture. She recognized two nepomorphan groups in this respect, viz. (1) those with an unmodified and distinct coxal cleft — *Ochterus* (Ochteridae), *Gelastocoris* (Gelastocoridae), *Notonecta* (Notonectidae), and *Hesperocorixa* (Corixidae), and (2) those with a modified coxal cleft — *Belostoma* and *Lethocerus* (Belostomatidae), *Aphelocheirus* (Aphelocheiridae), *Ambrysus* (Naucoridae), *Nepa* and *Ranatra* (Nepidae), and she noted that only in the belostomatids and naucorids the propleural supracoxal lobe is split to some extent. In the Pleidae the supracoxal cleft is slightly indicated but covered by a secondary prapleural exten-

sion. However, the groups recognized by Parsons (1967) have no phylogenetic significance: the taxa sub (1) are united by plesiomorphy, while the similarities shared by members of group (2) are surely partly homoplasic.

The architecture of the propleuron of the Helotrephidae is complicated by fusion of the head capsule with the prothorax, i.e., by evolution of the cephalothorax. Esaki & China (1928: p. 130, Fig. 1a) introduced a special nomenclature for "propleural" sclerites of the family, descriptive, but convenient and still in use. They have called the more mesally and ventrally situated sclerite fringing the proacetabulum a "propleural plate", and more marginally and laterally situated sclerite a "lateral pronotal plate". However, there are substantial differences among helotrephids in the Bauplan of the propleura.



Figs. 4, 5. *Helotrephes semiglobosus*. 4 — Anterior part of the left side of the body. Ventral view; legs removed. 5 — Left side of the pterothorax and base of abdomen. Ventral view; cephalothorax, legs and forewing removed. Dashed lines indicate the position of the metathoracic and first abdominal spiracles covered in ventral view by pleural sclerites.

The "propleural plate" in *H. semiglobosus* (Fig. 4) is represented by a ridge-like sclerite partly embracing the proacetabulum, and extending caudad into two processes. The broadly triangular "lateral pronotal plate" is distinctly delimited from the former sclerite and is situated lateroposteriad to it as an extension of the cephalic genal plate.

The propleuron of *D. stysi* (Fig. 7) is an extensive, non-subdivided, compact sclerite. The raised, ridge-like part corresponding to the "propleural plate" is only incipiently delimited from the "lateral pronotal plate" whose hind angle is situated strikingly caudad, approximately at the level of the anterior margin of the metathorax. An almost identical situation obtains in *T. compactus* (Fig. 8); the whole "propleural" region is concave, monolithic, without a distinct

border between the "propleural plate" and "lateral pronotal plate". The cuticle of the propleuron is covered in both species by a microplastron pilosity (cf. Parsons & Hewson, 1974: p. 515, Figs. 3—5).

The presence of the coxal cleft, a marker of the boundary between the episternum and epimeron, was not noted in any of the examined species. Hence the Helotrephidae fall in Parsons's (1987) 2nd group of nepomorphan families, characterized by a modified procoxal cleft. Homologies are difficult to establish here.

In considering the architecture of the helotrephid propleuron we should take into account 4 major alternatives, viz:

(1) propleural plate = proepisternum; lateral pronotal plate = proepimeron;
(2) propleural plate = proepisternum; lateral pronotal plate = proepimeron & ventrally reflected part of the pronotum;
(3) propleural plate = proepisternum & proepimeron; lateral pronotal plate = ventrally reflected part of the pronotum;
(4) propleural plate = proepimeron; lateral pronotal plate = ventrally reflected part of the pronotum.

The lateral pronotal plate is distinctly delimited in adult *H. semiglobosus*, and it is situated apart from the propleural plate (Fig. 4); the lateral sector of mesepisternum is extremely extended cephalad (reaching below the lobe-shaped genal plate of the head, cf. Figs. 4, 5), separating the propleural and lateral pronotal plates. The ventral part of the prothorax corresponding to the propleuron is entire, with no indication of the coxal cleft in 5th instar larvae of this species. On the other hand, the coxal cleft is distinct for a short stretch (anterolaterad to procoxal fovea) in 5th instar larvae of *T. compactus*, where it is evident that the proepisternal area of the propleuron is limited to a short triangular plate below the antennal tubercle of the cephalic region of the cephalothorax. A minute anterior to anterolateral emargination in the circumcoxal rim of the adults of *T. compactus* and *D. stysi* can perhaps be identified with the last vestige of the coxal cleft.

Consequently, the above hypothesis (3) seems most probable, and we interpret the "propleural plate" as being formed by the proepisternum (a very small, anterior part of the plate) & proepimeron, and the "lateral pronotal plate" as a ventrally reflected part of the pronotum (which might contain in the Limnotrephini and Trephotomasinae, also a lateral area of the proepimeron).

There are still other possible alternatives of sclerite homologies to be considered in the strongly apomorphic lateral cephalothoracic region of helotrephids. One of them is based merely on topography (see Fig. 4): "propleural plate" as a secondary sclerotization of apodemes belonging to the xiphal apparatus (sensu Puchkova, 1980); "genal plate" = genal plate s. str. fused with the proepisternum (forming the caudal lobe of the former); "lateral pronotal plate" = proepimeron.

Mesopleuron

An unusually extensive mesepisternum is characteristic of all the species studied; its lateral region extends in front of the ventral and lateral mesepimeral lobes and it is produced for the most part below the "lateral pronotal plate". This lateral mesepisternal part (relatively largest in *H. semiglobosus*, smallest in *T. compactus*) extends cephalad up to the head, partly even in front of the dorsal region of the mesepimeron similarly as in the Naucoridae (cf.

Parsons, 1970). The mesepisternum in *H. semiglobosus* bears long trichoid setae and continuous field of microtrichia (Pl. II, Figs. 1, 3—6), while only the microplastron cover is present in *D. stysi* and *T. compactus*. The ventrally situated part of the mesepisternum forms the roof of a ventromedially open air chamber of the mesothoracic spiracle; the floor and walls of this chamber are partly formed by the hind lobe of the "lateral pronotal plate" and by the anterior part of the ventral mesepimeral lobe.

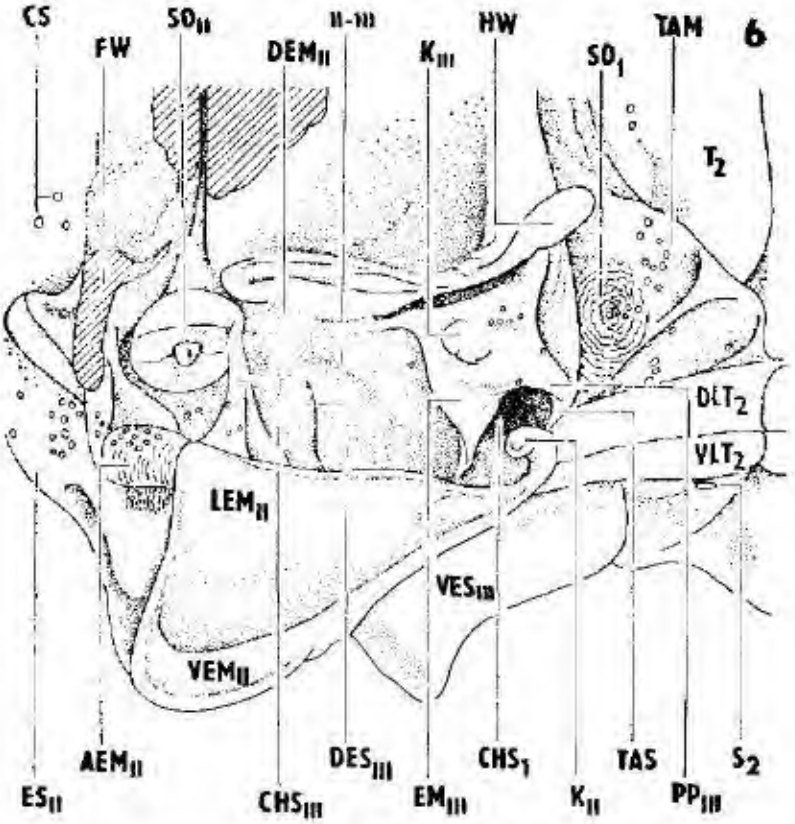


Fig. 6. *Helotrephes semiglobosus*. Lateral view of ventrolateral regions of pterothorax and first two abdominal segments. Hatched areas indicate a cut across the forewing and the area of pterothorax fused with the forewing, respectively.

The mesepimeron is an extensive and complex sclerite (Figs. 4—10). As in the other nepomorphans its anterodorsal part takes part in forming the mesothoracic postalar bridge. The circular to ellipsoid mesothoracic scolopophorous organ is situated in the latter region; in helotrephids, similarly as in the Aepheloheiridae and Naucoridae (cf. Parsons, 1974) and Pleidae (cf. Papáček, 1987), entirely surrounded by a collar-like postalar projection of the mesepimeron. In the dorsal part of the mesepimeron, below the above projection, there is an invagination so large that in the helotrephids it can be

characterized as the chamber of teh mesothoracic scolopophorous organ. The orientation of the surface the membrane of this organ is lateroventral in *H. semiglobosus* (Pl. I, Fig. 1), and for the most part in ventral in *D. stysi* and *T. compactus*; such orientation is shared with the Pleidae only (Papáček, 1987) while in the other Nepomorpha it is largely lateral. The collar-like projection is produced into an elongate lobe in *D. stysi* and *T. compactus* (Figs. 9, 10), covering the scolopophorous organ in lateral view. The chamber of this organ is more closed in *T. compactus* than in the other two species, laterally visible as a cuneiform crevice.

There is another deep invagination behind the chamber of the scolopophorous organ in a region formed by the posterodorsal part of the mesepimeron jointly with the dorsal part of the metepisternum. This invagination is directed antero-mesally, and functions as an air chamber of the metathoracic spiracle; it is broadly open in *H. semiglobosus* (Fig. 6), similarly as in the Pleidae, but its opening is narrower in *D. stysi* (Fig. 9), and the whole chamber is narrow, crevice-shaped in *T. compactus* (Fig. 10).

The ventrally situated part of the mesepimeron (Figs. 4—9) is formed by its ventral and lateral lobes, and it is shaped as a long, broadly triangular sclerite (called "supracoxal lobe" in other nepomorphans by various authors). The anterior margin of this sclerite has an angularly produced edge (Figs. 4, 7, 8) which in *D. stysi* and *T. compactus* partly overlaps the propleuron in the region of the "lateral pronotal plate". This overlap is also distinct in the specimens of *H. semiglobosus* fixed in ethanol or Bouin, but it is not apparent in dry material and in specimens prepared for SEM examination. The anterior outer angle of the ventral part of the mesepimeron is produced in anterior process in *H. semiglobosus* and *D. stysi*. In *H. semiglobosus* it is club-shaped, and its ventral surface bears a scale-like microsculpture (Pl. II, Fig. 1) which may function as a component of a stridulatory apparatus. The process is a smooth lobe in *D. stysi* and it is practically indistinguishable in *T. compactus*. The hind angle of the supracoxal mesepimeral lobe reaches below the metepimeron in *H. semiglobosus* and *D. stysi*, in *T. compactus* even more posterad, exceeding the latter caudally. In all the species studied this hind angle is produced in a dorsally to dorsolaterally directed wing-anchoring knob which jointly with the dorsal edge of the supracoxal lobe of the mesepimeron (Pl. II, Fig. 2) takes part in the fixation of the costal forewing edge by the mesepimeron.

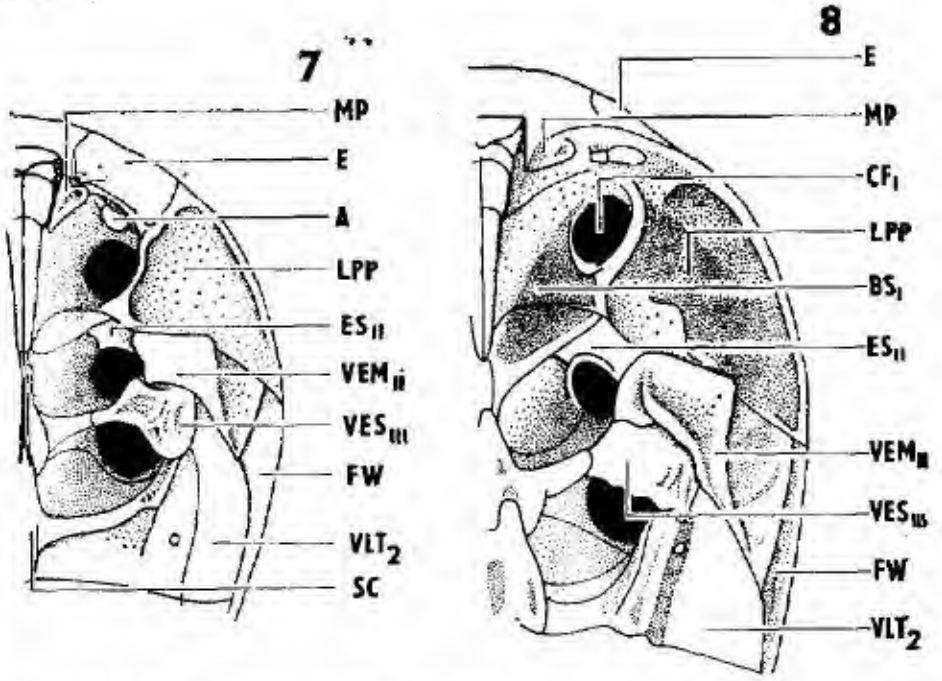
The dorsal part of the mesepimeron is continuously covered by plastron microtrichia, its ventral and lateral lobes are bare.

Metapleuron

The sulcus separating the mesopleuron from metapleuron (corresponding to an internal ridge) is laterally distinct in *H. semiglobusus* (Fig. 6), less distinct and shifted more cephalad in *D. stysi* (Fig. 9) and not apparent at all in *T. compactus*, since in the latter it runs at the bottom of a narrow invagination of the air chamber of the metathoracic spiracle in a region covered by the dorsal part of the mesepimeron.

The hindwings are mostly reduced (Figs. 8, 9, 10); their vestiges are membranous in *H. semiglobosus* and *T. compactus* which is also true of a small part of the metapleural axillary region. Hindwing vestiges and their axillary regions are sclerotized in *D. stysi*, and the reduced wings are partly fused to

the metathoracic notum. In those specimens of *H. semiglobosus* wiht non-reduced hindwnigs the axillary region of metapleuron is membranous, and its shape and size are identical with the situation obtaining in the Pleidae (cf. Papáček, 1987), while in the specimens with reduced hindwings the axillary region is relatively long and its longitudinal axis runs in anteroposterior direction. The longitudinal axis of this region is diagonal in the remaining two species, and it is directed dorso-caudad; its obliqueness is linked with a moderate shift of the dorsal parts of notal sclerites of the pterothorax caudad (Figs. 8, 9).



Figs. 7, 8. Anterior part of the body, left side. Ventral view; legs removed. 7 — *Distotrephes stysi*, 8 — *Trephotomas compactus*.

In the helotrephids as well as in the other aquatic bugs and the Gelastocoridae (cf. Parsons, 1960, 1974) the dorsal area of the mesepisternum takes part in forming the invagination of the air chamber of the metathoracic spiracle. The degree of metepisternal invagination differs: the invaginated area is formed by a relatively broad and for the most part lateral in *H. semiglobosus* and *D. stysi*, while in *T. compactus* (Fig. 10) it is formed by a narrow strip of cuticle facing cephalad to latero-cephalad owing to a deep invagination of the chamber. The ventral part of the metepisternum (= ventral metepisternal lobe) forms the supracoxale of the metacoxa; its position and general shape in the helotrephids is similar to other nepomorphans. However, while the coaptation of the metasupracoxale with the 2nd abdominal segment is markedly firm in the Pleidae (hind margin of the metasupracoxale fitting emarginations in the ridges of 2nd sternum and an emargination in the anterior projection

of the 2nd abdominal segment), it is looser in the Helotrephidae (only a close attachment to the groove of abdominal projection which is broader and shallower than in *Plea*).

A continuous layer of plastron microtrichia covers the whole ventral metepisternal lobe.

The metepimeron of the nepomorphans is a compact sclerite situated in the lateral metathoracic region and taking part in forming the metathoracic postalar bridge; this is also true of the helotrephids. The metepimeron of *H. semiglobosus* is square-shaped (similarly as in the Pleidae) (Fig. 6, Pl. I, Fig. 3), with an anterolateral process functioning as a metathoracic forewing-anchoring knob (Pl. I, Figs. 2, 3). The ventral angles of the metepimeron of this species are produced in bridge-like projections embracing an invagination functioning as an air chamber of the 1st abdominal spiracle. The projection of the anterior angle forms jointly with the anterior edge of the metepimeron the posterior margin of the air chamber of the metathoracic spiracle. The basic quadrangular shape of the metepimeron is modified in *D. stysi* (Fig. 9) by the invagination of its anterior ventral angle under the surface of the remaining part of the sclerite; the sunken part thus becomes the marginal part of the invagination of the air chamber of the metathoracic spiracle. Also in this species the metathoracic wing-anchoring knob projects laterad out of the surface of its metepimeron.

The metepimeron of *T. compactus* (Fig. 10) is roundedly triangular and lacks the forewing-anchoring knob*. The whole anterior ventral angle has become part of the deep invagination of the air chamber of the metathoracic spiracle and is not defined. There is no distinct boundary between the air chambers of the metathoracic and first abdominal spiracles, and both are interconnected in the lateral pterothoracic region. The hind ventral metepimeral angle forms in this species a broadly rounded posterior projection extending more ventrad than in the other two species. The hind margin of this projection is situated in *T. compactus* at the level of the wing-anchoring knob of the posterior corner of the ventral mesepimeral lobe, while it is situated considerably more caudad in *H. semiglobosus* and *D. stysi*, behind the mesothoracic wing-anchoring knob, almost in the region of the 2nd abdominal segment.

The metepimeron of the three helotrephids is covered by an almost continuous layer of plastron microtrichia (Pl. I, Figs. 2, 3).

The metathoracic scolopophorous organ is variously reduced in the Helotrephidae (particularly its membrane), and the extent of its reduction seems to be linked with the degree of reduction of the hindwings and sclerotization of the originally membranous axillary metapleural region. The organ in Nepomorpha (including the Pleidae) is situated in a membranous region near the upper margin of the metepimeron below the hindwing (Larsén, 1957; Papáček, 1987; Parsons, 1974). This is also true of the individuals of *H. semiglobosus* with non-reduced hindwings, and this organ, seen as small scolops knob within a depigmented cuticular field, is distinguishable also in helotrephids with reduced hindwings, but it is smaller and less differentiated. In *D. stysi*, within the corresponding part of the sclerotized cuticle, there is only a small tubercle which can be identified as a vestige of the scolops knob; the membrane is absent altogether. The structure is hardly identifiable in *T. compactus* and it merges with the surrounding membranous cuticle; the knob is desclerotized and non-pigmented.

*) Almost the whole metepimeron as well as the axillary region of hindwings are covered by the cephalonotum in *T. compactus* (cf. Figs. 3, 10, and Pl. I, Fig. 4).

Lateral thoracico-abdominal junction

General structure in the Nepomorpha. The thoracico-abdominal junction is formed by fusion of the 1st abdominal segment with the metathorax; the area of fusion including the 2nd abdominal segment is also called a "thoracico-abdominal region" (sensu Parsons, 1976). The laterodorsal area of fusion, situated closely behind the 3rd thoracic phragma, is membranous (= "functional thoracico-abdominal membrane", Parsons, 1976). This membrane is partly formed by a desclerotized part of the 1st abdominal tergum (dorsally and dorsolate-

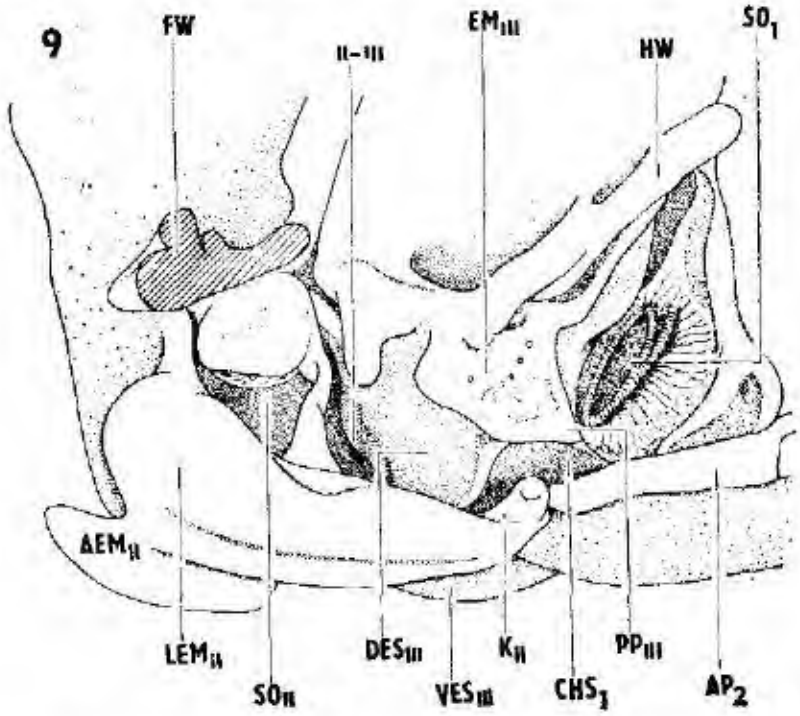


Fig. 9. *Distotrephes stysi*. Lateral view of the ventrolateral regions of pterothorax and first two abdominal segments.

rally), and partly by a membranous region between the 1st and 2nd abdominal segments (laterally); dorsal and dorsolateral parts of tergum 1 may be for the most part retained as a distinct sclerite (cf. Parsons, 1970, 1976). The thoracico-abdominal membrane is anteriorly continuous with the metathoracic postnotum (Parsons, 1976), and its extent is variable at the genus level; owing to the existence of this membrane and a frequent reduction of the 1st abdominal sternum, the delimitation of the metathorax from the abdomen is indistinct.

The lateral part of the thoracico-abdominal membrane is produced caudad into the area of 2nd abdominal tergum, and the scolopophorous organ* of 1st abdominal segment is situated within this membranous projection. In the nepomorphan species studied so far it has the shape of a small knob without a well defined surrounding membrane (Larsén, 1957; Papáček, 1987).

* The term scolopophorous organ of the first abdominal segment is used here and throughout the text for the discolopodial organs sensu Larsén (1957).

The ventrolateral part of the thoracico-abdominal junction is formed by a narrow thoracico-abdominal sclerite (Parsons, 1970 and others) covered partly by the posterior lobe of metepimeron, and partly by the anterior projection of the 2nd abdominal segment. The origin of this structure is not clear. Larsén (1945 a) takes it for part of the 1st abdominal sternum, Parsons (1976) for a derivate of the metepimeron, but in her earlier papers she allowed for its abdominal origin and remarked that it may be partly abdominal and partly thoracic (Parsons, 1971). Papáček's (1987) opinion is that its major part is abdominal in the Pleidae.

The thoracico-abdominal sclerite of many nepomorphans is completely or partly covered laterally by the anterior projection of the 2nd abdominal segment formed by the laterotergite (subdivided often into ventral and dorsal laterotergites) associated with the sternum, and pointing cephalad-like a dome or spine. This projection is relatively shortest in the Corixidae (not extending cephalad onto the metathoracic region and not reaching the level of the anterior margin of abdominal tergum 1) and longest in the Naucoroidea and Pleidae (extending onto the metathoracic region and exceeding cephalad the anterior margin of abdominal tergum 1). In latter family it even contacts the hind angle of the supracoxal mesepimeral lobe and is uniquely provided with a third forewing-anchoring knob (Papáček, 1987).

Helotrephidae. The anterior projections of the 2nd obdominal segment is identically constructed in all our helotrephids studied: broadly-shaped,

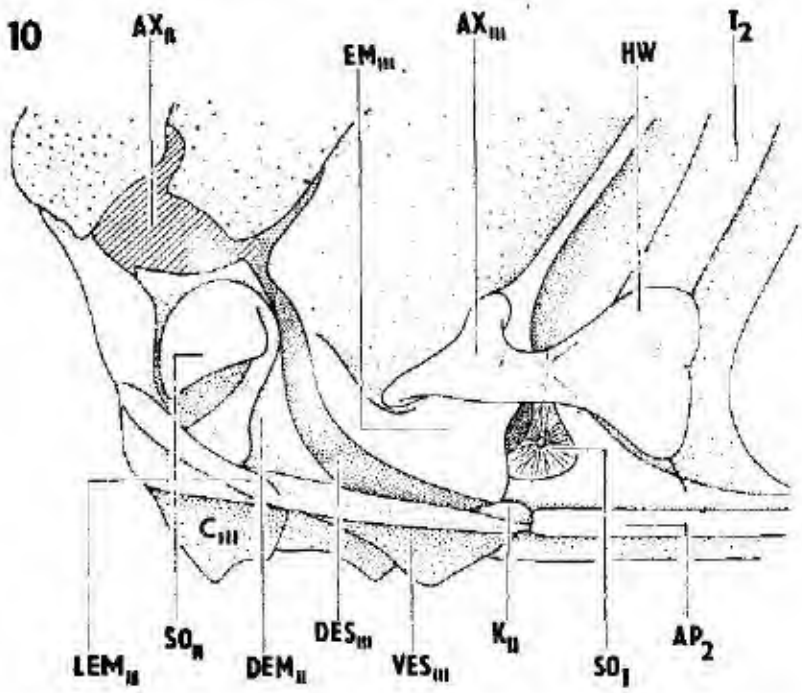


Fig. 10. *Trephotomas compactus*. Lateral view of the ventrolateral regions of pterothorax and first two abdominal segments.

extending cephalad below the metepimeron, and contacting and being even slightly overlapped by the hind angle of the supracoxal mesepimeral lobe. In

all these extreme features it resembles that of the Pleidae, only the pleid forewing-anchoring knob is missing.

The dorsolateral area of the functional thoracico-abdominal membrane is developed in the Helotrephidae as in other Nepomorpha. However, it is more extensive in the region of the scolopophorous organ of the 1st abdominal segment. Here in *H. semiglobosus* the membrane turns into a plicate rim situated closely above the anterior projection of the 2nd abdominal segment (Fig. 6; Pl. I, Fig. 2). The rim is covered by microtrichia, and represents undoubtedly a part of the secondarily sclerotized thoracico-abdominal membrane. The scolopophorous organ is externally provided with a moderately expressed scolops knob surrounded by deeply and irregularly circularly plicate membrane (by a larger size and presence of plicate the organ differs from the situation in the Pleidae — cf. Papáček (1987)). The organ is situated in a shallow concavity and its diameter is shorter than the height of the metepimeron.

In *D. stysi* the scolopophorous organ is more sunken between the metepimeron and 2nd abdominal tergum than in the former species, and its diameter is somewhat larger than the height of the metepimeron (Fig. 9). Its membrane is plicate and attached to an irregular central structure. The situation in *T. compactus* resembles the mesothoracic scolopophorous organ — the central scolops knob is distinct, and the membrane densely radially plicate (Fig. 10; Pl. I, Figs. 4—6). The similarity is enhanced by the presence of a partly closed chamber of the scolopophorous organ of the 1st abdominal segment; its opening is delimited by the hind margin of the metepimeron and the anterior edge of the emargination of a secondary sclerotization of the 2nd abdominal tergum.

The thoracico-abdominal sclerite is distinct and laterally visible in *H. semiglobosus* (Pl. I, Fig. 3) and *D. stysi;* it forms the posterodorsal wall of the air chamber of the 1st abdominal spiracle in the area of the posterior lobe of metepimeron. Most of the surface of this sclerite faces lateroventrad to ventrad, and its cuticle is continuous with that of the abdomen mesad of the abdominal projection. The thoracico-abdominal sclerite is not visible in lateral view in *T. compactus*, because it is covered by the posterior lobe of the metepimeron; most of its surface faces ventrad.

Position of spiracles

The mesothoracic spiracle

of nepomorphans (excepting the Pleidae) is situated in the intersegmental pro-mesothoracic membrane.

However, in the 3 helotrephids it is situated intrasegmentally, in the sclerotized region of the anterior margin of the mesepisternum (Fig. 5). In *H. semiglobosus* the spiracle is in the most lateral position, and it is large, ellipsoid, with a system of trabecular ribs. In *D. stysi* and *T. compactus* it is smaller and situated more mesally. Its intrasegmental position in the Helotrephidae is similar to the Pleidae where the first thoracic spiracle is situated in a narrow sclerotized trough of the mesepisternum close to the intersegmental membrane.

The metathoracic spiracle.

The second thoracic spiracle is metathoracic in origin, but in the Nepomorpha is situated either intersegmentally (at the border between lateroventrally to ventrally situated regions of he dorsal parts of the mesepimeron and metepisternum) or shifted onto the mesothorax, being then situated near the hind margin of the dorsal part of the mesepimeron which takes part in forming the shallow deep pleural in-

Table 1. Typology of the metathoracic spiracle of Nepomorpha
Based on Parsons (1974), Papáček (1987 — Pleidae), and Rawat (1939 — Ilyocoris); for Helotrephidae see the text, situation in the Ochteridae and Potamocoridae unknown.

Type	S_1	S_2	S_3	S_4
(1) Location	mesepimeral to intersegmental	intersegmental	mesepimeral	mesepimeral
(2) Air space into which it opens	lateral intersegmental	ventral intersegmental	subalar	lateral intersegmental (and subalar)
(3) Position	lateroventral	ventral	lateral	lateral to lateroventral
(4) Covered by lateral lobe of mesepimeron	yes	yes	yes, or freely visible in lateral view*	yes
Occurrence	Nepidae, Belostomatidae, Gelastocoridae, Aphelocheiridae, Naucoridae part. (Ambrysus, Heleocoris, Ilyocoris, Pelocoris), Helotrephidae	Naucoridae part. (Cryphocricos, Limnocoris)	Notonectidae, Corixidae	Pleidae

*) Legend: Notonectidae: spiracle large, dorsoventrally elongate, its major part well visible in lateral view; Corixidae: spiracle smaller (size variable), rounded, laterally fully (Diaprepocoris) or partly (Corixinae) visible or fully covered (Cymatiainae, Micronectinae) by the lateral lobe of the mesepimeron, but always visible in dorsolateral view.

vagination of the air chamber. Parsons (1974) distinguished three types of the nepomorphan metathoracic spiracle (termed S_1, S_2, S_3). The typology is reviewed in Table 1; also the riparial Gelastocoridae fit the scheme. Papáček (1987) concluded that the situation in *Plea minutissima* (Leach) is a borderline case of S_{1-2} or an extreme S_3 situation; here we prefer to classify it as a separate type S_4. It also differs from S_3 by its small size and ventral position (corresponding to the ventralmost part of the large notonectid spiracle).

In the three helotrephids the spiracle is intersegmental, being situated in a deep pleural invagination covered by the lateral lobe of the mesepimeron (cf. Fig. 5) and hence not visible in lateral view. It is situated lateroventrally (laterally to lateroventrally in the Pleidae) and opens into the lateral intersegmental air space. The degree of communication between the lateral and subalar air spaces depends on the genus-specific degree of the depth of the invagination (shallowest and widest in *H. semiglobosus*, deepest and narrowest in *T. compactus*). The spiracle is situated more ventrad than in the Pleidae and its size and position are comparable to those described and illustrated by Parsons (1974) in *Pelocoris femoratus* (Palisot de Beauvous) and *Ambrysus teutonicus* La Rivers (Naucoridae). In all respect the Helotrephidae fall into the S_1 group and differ considerably from the Pleidae and even more from the Notonectidae.

Spiracle of the first abdominal segment

is situated in most nepomorphans on the thoracico-abdominal sclerite, i.e., in an intersegmental position in the region of the thoracico-abdominal junction. (In the Notonectidae the spiracle is situated in a membrane forming a ventral continuation of the thoracico-abdominal sclerite; this membrane has been called a "metacoxal mebrane" by Parsons (1970), but it can possibly represent a membranous continuation of the thoracico-abdominal sclerite.) One of the extreme positions, the most lateral and dorsal, is exhibited by the Corixidae: their thoracico-abdominal sclerite is situated more dorsad than the posterior lobe of the mesepimreon, turning *smoothly into a functional thoracico-abdominal membrane, and in some species it* is partly or completely (secondarily?) membranous.

The other extreme situation is exhibited by the Pleidae and Helotrephidae where the 1ts abdominal spiracle is ventral. In *H. semiglobosus* and *D. stysi* it is situated in the dorsal wall of the air chamber which is located ventrad of the metepimeron and opens laterally into the subalar air space (Figs. 6, 9; Pl. I, Fig. 2); either there is no communication with the air chamber of the metathoracic spiracle (both chambers being separated by the anterior lower angle of the metepimeron like in the Pleidae), or it is realized by an extremely narrow crevice below the hemelytron. The air chamber of this spiracle is low and crewice-shaped in *T. compactus* (Fig. 10; Pl. I, Fig. 4), communicating with the air chamber of the metathoracic spiracle and with the subalar air space by narrow air channels. The spiracle is shifted so much ventrad in the three species that it is situated more mesally than the anterior projection of the 2nd abdominal segment, under the posterior external angle of the ventral metepisternal lobe. When the abdomen is torn off from the thorax during dissection the thoracico-abdominal sclerite mostly remains attached to the abdomen, and it seems to represent an antrolateral continuation of a narrow basiabdominal sclerotization covered by metacoxae and possibly representing a reduced first abdominal sternum. Esaki & China (1927; p. 287, Figs. 6a, c) in *Idiocoris lithophilus* and *Paskia minutissima* (Idiocorinae), and Miyamoto (1952; Pl. 3, Figs. B, F) in *Helotrephes formosanus* illustrated the position of the first abdominal spiracle as ventral and "strictly abdominal".

Consequently, the first abdominal spiracles of the Helotrephidae (as well as those of the Pleidae — see Papáček (1985, 1987)) can be called "intersegmental" only by virtue of their situation on the thoracico-abdominal sclerite which is intersegmental by name and definition; actually, they are abdominal and hence intrasegmental, being associated with likely vestiges of the first abdominal segment. The thoracico-abdominal sclerites, associated with the vestigial first abdominal sternum, can be interpreted as possible remnants of laterotergite of the first abdominal segment.

Thoracic air stores

The air stores and the extent of a renewable air-bubble in aquatic Heteroptera have been described by many authors, recently by Parsons (1976). In the Notonectidae and Pleidae the air-bubble is situated on the ventral body surface and in the subalar space; moreover, a supra-alar air store is maintained in the notonectids. The ventral air-bubble of the Notonectidae is maintained by hydrofuge macrochaetae all over the ventral surface of the abdomen and the thorax including the entire vetrally situated pleural area. In all Pleidae the ventral air-bubble covers the whole abdominal venter (being maintained mainly by hydrofuge macrotrichia), and either the whole or only part of the ventral thoracic surface. In the Palearctic *Plea minutissima* the ventral thoracic air store is situated in the sternal region (being maintained mainly by coxal and basisternal macrotrichia) and in the ventral

part of the propleuron and metapleuron (i.e. proepisternum & proepimeron and ventral metepisternal lobe) where it is maintained by a continuous microtrichial field. The air-bubble never covers the bare supracoxal mesepimeral lobe (Papáček, 1985). Such situation apparently does not occur in whole family. Gittelman (1975; p. 1015, Figs. 2—5) illustrated the ventral air-bubble in the Nearctic *Neoplea striola* (Fieber) as being maintained all over the ventral surface of the thorax (including the supracoxal mesepimeral lobe) by marginal macrotrichia (the latter are definitely missing in adults of *Plea minutissima*).

We could not study the ventral air stores of the Helotrephidae in living specimens, and had to assess their extents according to the distribution of hydrofuge macrotrichia and microtrichia (Pl. II, Figs. 3—6). The situation seems to be identical with (abdomen) or very similar to (thorax) *Plea minutissima*. In particular, the air-bubble cannot be maintained over the bare supracoxal mesepimeral lobe (lacking both the macro- and microtrichia). In *H. semiglobosus* the air-bubble cannot cover the entirely bare surface of the lateral pronotal plate (supported by an illustration of the "outline of the plastron when the insect is submerged" in *Helotrephes formosanus* by Miyamoto (1952; Pl. I, Figs. A, B). On the other hand, the concave part of the "propleuron" of *D. stysi* and *T. compactus* probably forms a part of the ventral air store, since only the marginal part of the "propleuron" is entirely bare, even without microtrichia.

The mesothoracic spiracle of the helotrephids is situated at the anterior margin of the mesepisternum in a region covered by microtrichia and hence (as in the pleids) within the area covered by the air-bubble. The microtrichial field of the mesepisternum which is laterally covered by both the mesepimeral supracoxal lobe and the lateral pronotal plate mainatins in *H. semiglobosus* (and probably in all the Helotrephini?) a broad air channel connecting the ventral air store with the dorsolateral subalar air store as in the Pleidae. In *D. stysi* (and probably in all Limnotrephini?) and *T. compactus* this channel either does not exist at all or it is extremely narrow owing to a close union of the propleuron, mesepisternum and supracoxal lobe of the mesepimeron (Figs. 7, 8); the latter alternative is more probable since the sclerites concerned are covered by microtrichia even on the undersurface. Another possible connection (as in the pleids) between the ventral thoracic and subalar air stores may be realized through a narrow air channel in the metacoxal region through the air chamber of the 1st abdominal spiracle.

Stridulatory apparatus

We are uncertain about the real situation since three different couples of structures (indicated A, B, C, respectively) might be involved in strigilation in the helotrephids.

(A) In the Pleidae the stridulatory apparatus is formed by pectinately arranged cuticular scale-like structures on the mesepisternum (stridulitrum) and the hind margin of the proepimeral lobe (plectrum) according to Wefelscheid (1912) and Papáček (1985). Miyamoto (1952) remarked on *Helotrephes formosanus* that "The stridulatory organ is similar to that of *Plea* in structure, but it is more closely situated to the lateral margin of the body..." (an observation based probably on Wefelscheid (1912)). Rieger (1976) regarded the position of the stridulatory apparatus in the Pleidae & Helotrephidae as a synapomorphy of these families. We have found in *H. semiglobosus* an extensive area with a scale-like microsculpture in the ante-

rior part of the mesepisternum (Fig. 5; Pl. II, Fig. 3) and on the anterior process of the supracoxal mesepimeral lobe, i.e., in positions corresponding to the stridulitrum of *Plea*. If the organ is functional we assume that the function of the plectrum can be performed either by the hind margin of the lateral proontal plate or by the hind margin of the propleural or pronotal plate. No similar structures were found in *D. stysi* and *T. compactus*.

Polhemus (1990) has stated that the Helotrephini and Limnotrephini (Helotrephinae) differ in the type of their stridulatory apparatus, different from (A) in both cases. (B): Helotrephini: stridulitrum — serration of the costal margin of the hemelytron, plectrum — a distal ridge of the hind femur. (C): Limnotrephini: stridulitrum — a row of denticles on the dorsal surface of the hemelytron, plectrum — ridges/denticles under the posterior margin of the cephalonotum. However, Polhemus (1990) has observed at the same time that the base of hemelytron of *Hydrotrephes* (Helotrephini) is provided with the same (homologous) structures (C) as in the Limnotrephini, concluded that regardless whether these structures function as sensory organs or take part in strigilation or wing-locking, their presence in both tribes suggests that they can be considered a synapomorphic character of the subfamily Helotrephinae. Papáček, Štys & Tonner (1988; Pl. III, Fig. 4) have illustrated a tuberculate surface of the hind femur of *T. compactus* (Trephotomasinae); it is a femoral plectrum involved in strigilation of the (B) type or the vestige of such a structure. (We cannot exclude that a quite different, unique stridulatory apparatus is involved; the matter is under investigation).

The presently available data (there is no information on the Helotrephidae: Neotrephinae and Idiocorinae) suggest the following distribution of structures considered as taking part in strigilation: (A) Pleidae and Helotrephini; (B) Helotrephini and possibly the Trephotomasinae; (C) Limnotrephini. (Existence of two different kinds of stridulatory apparatus in the Helotrephini is, however suspicious on a priori grounds.) However, more structural and functional information is necessary for assessment of these data within the cladistic context.

COMPARATIVE CONCLUSIONS

Although many scattered comparative data have already been summed up in the previous section, we wish to emphasize the newly discovered features which either document the consequences of evolution of the compact cephalothorax and posterior extension of the cephalonotum over the pteronotum in the Helotrephidae, or other unique characters of this family, or point out its similarity with the Pleidae.

(1) Fixation of forewings to the cephalonotum. In Nepomorpha other than Pleoidea the posterior margin of the pronotum extends over the bases of forewings usually moderately, in some cases considerably (e.g. some Corixidae), but never restricts the forewing mobility. However, in the Pleidae the upper surface of forewing bases is coapted with the undersurface of the extended pronotum, and the forewings are thus fixed to the body (Papáček, 1985). In the helotrephids with micropterous hindwings the forewings fuse with undersurface of the cephalonotum covering large proximal sectors of the forewings, and the latter are immobilized and tightly cover the subalar space.

(2) Propleuron*. The ventrally situated helotrephid propleuron also probably includes part of the ventrally reflected pronotum which can be either distinctly delimited (as "lateral pronotal plate") or amalgamated with the propimeron. A similar "ventral reflexion" of pronotal areas occurs in the Pleidae (Papáček, 1985; p. 205, Fig. 2). The proepimeral cuticular area is reduced in the helotrephids to a small ridge-like sclerite reflected ventrolaterad and forming a part of the "propleural plate". A similar tendency to the transformation of the proepimeron into a ridge is exhibited by the Pleidae (cf. Papáček, 1987) and also by the Aphelocheiridae (cf. Popov, 1971; Fig. 43), while in most of the other Nepomorpha the proepimeron has the usual heteropteran shape of a flat sclerite extending caudad into a lobe (the lobe is not developed in the Ochteroidea — see Popov, 1971; Figs. 35, 36).

(3) Shortening of the pterothorax. The dorsal parts of the pterothoracic pleurites are strongly abbreviated along the anteroposterior axis (a similar situation exists in the Pleidae only), undoubtedly owing to extension of the cephalonotum over the pterothorax; it seems as if they would be compressed between the expanding cephalonotum and relatively well developed basal abdominal segments. Another effects excerted by the cephalothorax on the pteropleuron is seen in the degree of the pleural invagination of the air chamber of the metathoracic spiracle — the longer the cephalonotum the deeper is this invagination.

(4) Mesepimeron. The largest sclerite of the ventral region of the pleuron is the ventral & lateral part of the mesepimeron in both the Pleidae and Helotrephidae. The anterior margin of the ventral mesepimeral lobe extends considerably over the propleuron in the Pleidae, but in the Helotrephidae it only touches it or extendings over it slightly. The air-buble is not maintained over the ventral part of the mesepimeron in the Helotrephidae and some Pleidae (in contrast, e.g., to the Notonectidae).

(5) The forewing-anchoring knob of the ventral mesepimeral lobe serves for fixation of the forewing while at rest in all the Nepomorpha (even in those with reduced forewings, e.g., in micropterous *Aphelocheirus* — cf. Parsons (1974)). However, the forewing-anchoring knob of the metepimeron is developed only in the Pleidae (cf. Papáček, 1985, 1987; Popov, 1971; Puchkova, 1980) and Helotrephidae. Its absence in *Trephotomas compactus* is autapomorphic, and its function is substituted by the fixative capability of the long cephalonotum extending over the metepimeron.

(6) Metathoracic spiracle. The typology and taxonomic distribution of types S_1—S_5 has been reviewed in the descriptive part. While the spiracle of the Notonectidae (together with that of the Corixidae) belongs to type S_3, the Pleidae posses an autapomorphic type S_4, and the Helotrephidae share type S_5, which is probably plesiomorphic in terms of the Nepomorpha, with most of the other Nepomorpha (including some of the Naucoridae).

(6) Thoracico-abdominal junction exhibits in the Nepomorpha two extreme conditions represented by the Corixidae (membrane behind the 3rd phragma relatively broad; scolopophorous organ of the 1st abdominal segment very small (= discolopodial organ), hardly distinct; spiracle of the 1st abdominal segment extremely dorsal; not even vestiges of abdominal sternum

*Note that some alternative homologies for the structures discussed below have been suggested in the descriptive part.

1 present) and Helotrephidae (dorsolateral and lateral parts of the membrane mostly invaginated behind the 3rd phragma, broad only caudad to metepimeron where it bears a large scolopophorous organ with a chamber; spiracle of the 1st abdominal segment extremely ventral; sternum 1 retained).

The relatively large size of the scolopophorous organ of the 1st abdominal segment and particularly the apparently synapomorphic presence of its chamber in the Helotrephidae are unique in Heteroptera. In *T. compactus* the organ is structurally comparable to the mesothoracic one (situated in a laterally covered invagination like in all helotrephids), and it is even larger.

The *metathoracic scolopophorous organ* is reduced in the helotrephids (similarly to the situation in macropterous *Aphelocheirus* — cf. Parsons (1969)) compared with the other nepomorphans, obviously concomitantly with the reduction of hindwings and sclerotization of their axillary region. On the other hand, the large organ of the 1st abdominal segment probably is of a greater functional importance in the helotrephids than in the other nepomorphans (cf., e.g., Prager & Streng, 1982) owing to its broad contact with subalar air space.

We have already argued in the descriptive part that the thoracico-abdominal sclerite is probably an abdominal structure, at least in the Helotrephidae and Pleidae, and hence the 1st abdominal spiracle actually is intrasegmental rather than intersegmental (its intrasegmental position has been noted in the first instar of *Plea minutissima* by Cobben, 1978). It remains to be seen how much of this observation can be extended to other Nepomorpha.

The absence of the 1st abdominal sternum (or its incorporation into the metathoracic endoskeleton) has often been claimed to be a groundplan character of the Heteroptera, and most of the modern students of insect phylogeny believe that it is a synapomorphy of all Acercaria (= Paraneoptera without Zoraptera). Štys (1985) has refuted this generalization. In Heteroptera the 1st abdominal sternum has been observed in several groups of Enicocephalomorpha (references by Štys, 1985), in primitive Gerridae of the Geromorpha (Matsuda, 1960; Møller-Andersen, 1982), in Leptopodomorpha (Cobben, 1978), and also in various Nepomorpha: in the Helotrephidae (this study), Pleidae (*Plea* - Papáček, 1985, 1987; Wefelscheid, 1912), Notonectidae (*Notonecta* — Hoppe, 1912; *Buenoa* — Bare, 1928) and Naucoridae (*Ilyocoris* — Rawat, 1939). Retention of this sclerite must be the case, since so many reversals to re-appearance of this structure are improbable.

(7) Notes on relationships. Higher classification of the Helotrephidae in its present form has been established by Papáček, Štys & Tonner (1988) and Polhemus (1990), viz.: 1. Neotrephinae, 2. Trephotomasinae, 3. Helotrephinae (Helotrephini, Limnotrephini), 4. Idiocorinae. Further consideration of the relationships of these taxa and final assessment whether the Pleidae and Helotrephidae are adelphotaxa must wait until the Neotrephinae and Idiocorinae will have been re-examined, and until new critical Neotropic genera will have been described (J. T. Polhemus *in prep.*). The Helotrephidae are certainly a much more variable group than the Pleidae, and only few helotrephid characters are uniform (e.g., distribution of air stores) and show constant and possibly synapomorphic differences from the latter family (e.g., type of the metathoracic spiracle, presence of air chamber of the first abdominal discolopodial scolopophorous organ, adult cephalonotum).

On the other hand, we not doubt that the Pleidae & Helotrephidae (i.e.

Pleoidea sensu Štys & Jansson, 1988) are monophyletic. We can support this conclusion by the following incomplete list of pleoid synapomorphies:

1. At least partial fusion of the head and prothorax, at least in larvae (for details see Papáček, Štys & Tonner, 1990).
2. Larval atennae non-segmented, developed as non-articulating antennal tubercles.
3. Membrane of forewings reduced (Papáček, 1985).
4. Two pairs of leaf-like sensilla apically on the last tarsites of all pairs of legs (Papáček, 1985).
5. Deep invagination of lateral surface of the pterothoracic pleura and shortening of the pterothorax.
6. Lateroventral to ventral orientation of the membrane of the mesothoracic scolopophorous organ.
7. Ventral orientation of most of the surface of the thoracico-abdominal sclerite as well as of the first abdominal spiracle.
8. Additional forewing-anchoring knob present on the metepimeron (secondarily absent in the Trephotomasinae).
9. The ventral part of mesepimeron contacting or overlapping the propleuron.
10. Unpaired orifice of the larval dorso-abdominal scent gland opening between segments 3/4 only (China, 1940). (Homoplasic loss of scent gland system: Ochteroidea, Nepoidea, Notonectidae; plesiomorphic retention of gland orifices at three intersegmental boundaries: Corixidae; reduction to position 3/4: Naucoroidea, Pleoidea; paired condition: Aphelochiridae, Naucoridae — symplesiomorphy in terms of Naucoroidea & Pleoidea; unpaired condition: Potamocoridae (cf. Cobben, 1978) and Pleoidea — probably a homoplasic similarity).
11. Body minute.

We have recently (Papáček, Štys & Tonner, 1988) pointed out some characters shared by the Pleoidea and Naucoroidea and not occurring in the Notonectidae; to these we can add a possibly synapomorphic presence of a closed collar-like projection of the dorsal mesepimeral lobe surrounding the mesothoracic scolopophorous organ. Similarities in the communication of the metathoracic spiracle with the air stores and retention of larval dorso-abdominal gland system are, however, undoubtedly of plesiomorphic nature in terms of the aquatic Heteroptera.

Explanation of figure lettering

A	= antenna
ABD	= abdomen
AEM_{II}	= anterior process of mesepimeron
AP_2	= lateral anterior projection of the second abdominal segment (= abdominal projection of the second abdominal segment (Parsons, 1976)
$AX_{II,III}$	= axillary region of mesothoracic wing (forewing) and metathoracic wing (hindwing)
$BS_{I,II}$	= prothoracic, mesothoracic basisternum
C_{III}	= midsternal metathoracic carina
CF_I	= coxal fovea of prothorax
CFW	= clavulus of forewing
$CHS_{III,1}$	= air chamber of the metathoracic or first abdominal spiracle
CN	= cephalonotum
CS	= campaniform sensilae

CX	= metacoxa
DLT_2	= dorsal laterotergite of adbominal segment 2
D, L, V EM_{II}	= dorsal, lateral and ventral lobe (part) of mesothoracic epimeron (L & V EM_{II} = supracoxal lobe of mesepimeron)
D, L, V ES_{III}	= dorsal, lateral and ventral lobe (part) of metathoracic episternum
E	= eye
EM_{III}	= metathoracic epimeron
ES_{II}	= mesothoracic episternum
FW	= forewing
GP	= genal plate
HW	= hindwing
K_{II}	= wing-anchoring (forewing-anchoring) knob of the posterior corner of supracoxal (ventral) mesepimeral lobe
K_{III}	= forewing-anchoring (wing-anchoring) knob of metepimeron
LFW	= left forewing
LPP	= lateral pronotal plate
LR	= lateral ridge of mesothoracic epimeron
M_{I-II}	= membrane between pro- and mesothorax
MP	= maxillary plate
$N_{II,III}$	= mesonotum, metanotum
PP	= propleural (pleural) plate
PP_{III}	= posterior projection or lobe of metepimeron
PS_{II}	= mesothoracic prescutum
RFW	= right forewing
$S_{II, 1, 2}$	= mesothoracic, first or second abdominal spiracle
SC	= sternal carina
SC_{II}	= mesothoracic scutum
SCT	= mesothoracic scutellum
$SO_{II,III,1}$	= scolopophorous organ of mesothorax, metathorax or discolopodial scolopophorous organ of abdominal segment 1
ST_2	= sternum of abdominal segment 2
$T_{1,2}$	= tergum of abdominal segments 1, 2
TAM	= functional thoracico-abdominal membrane
TAS	= thoracico-abdominal sclerite
$VLT_{2,3}$	= ventral laterotergite of abdominal segment 2 or 3
II-III	= lateral ridge between meso- and metathorax

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SCANNING ELECTRON MICROSCOPY OF ASCARIS TARBAGAN (NEMATODA)

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Abstract. Scanning electron microscopy (SEM) was used for the first time for examinations of the species *A. tarbagan* Schulz, 1931, whose systematic position has often been discussed in literature. For the first time the description gives the number of denticles in the lips, the structure of the doubled and simple papillae on the lips, and the surface of the body and spicules is described in greater detail. In the males, no rugose ornament was found around the cloaca. The eggs have a firm envelope without an expressive net-like structure. Given are also data about the systematic-taxonomic classification of *A. tarbagan*.

In order to precise the knowledge about some morphological characters of the species *A. tarbagan* Schulz, 1931, and to help to solve its so often discussed taxonomical position (survey see Hartwich 1975), the SEM was used for the investigations.

MATERIAL AND METHODS

Investigations were carried out with 3 females and one male of the species *A. tarbagan*. The material was obtained from dissection of *Marmota sibirica* from the region of the Baykal basin, USSR. The material was fixed in 10% formaldehyde and evaluated on the basis of data from Mozgovoy (1951), Ryzhikov et al. (1979) under an optical microscope. For SEM examinations the specimens were then dehydrated through an ethanol series and subjected to ultrasound for one minute in absolute ethanol. Then they were critical-point dried, mounted on a double-side tape, coated with gold and examined in a Jeol JSM - S1 microscope.

RESULTS

At the end of the head part without lateral alae there were three great lips (Fig. 1).* On the internal edges of the lips there are 66—72 shallow denticles (Figs. 2, 3). The dorsal lip has two doubled papillae (Fig. 5), the lateroventral lips have one doubled and one simple papilla (Fig. 4). The male was 48 mm long, the maximum width was 1.5 mm. The abdomen of the body was curved ventrally, the cloaca was 0.45 mm from the end of the body (Fig. 8). There is no rugose or other ornamentation around the cloaca (Fig. 9). There are 2 spicules of the same length of about 0.42 mm ended in a blunt tip (Fig. 9). The surface of the spicules is not smooth, it is undulated (Fig. 10). The female was 110—150 mm long, the maximum width was 2.6 mm. The vulva was situated in the anterior fourth of the body. The abdomen was straight, conical, with an anal opening (Fig. 7). The eggs have a firm envelope without an expressive

*The figures 1—12 (Plates I—III) will be found at the end of this issue.

net-like structure (Fig. 6). On the surface of the body is a complex of stripes, of which 9—11 stripes form a separate bundle which is divided by a marked groove (Figs. 11, 12).

Notes on the taxonomy of *A. tarbagan* Schulz, 1931

Opinions on the systematic-taxonomical position of the species *A. tarbagan* are not uniform what is evident from the following history:

Linstow (1897) (ex Hartwich 1975) found nematodes in *Marmota monax* (locality of the zoological gardens in Königsberg) which he named *Ascaris pigmentata*. It is not known if this material has been preserved.

Leidy (1856) (ex Hartwich 1975) described the species *Ascaris laevis* which the above author reported as being a parasite of marmots (*Marmota*) and ground squirrels in North America and in the USSR and which had been frequently found also in the Alps in Switzerland. He does not exclude the occurrence of the parasite in *M. marmota* in the German Alps in the same host. Tiner (1951) elaborated the morphology of the species *A. laevis* in greater detail. Characteristic of this species is the male has a markedly rugose ornamentation around the cloaca.

Schulz (1931) described the species *Ascaris tarbagan* from rodents of the genus *Marmota* from the territory of the USSR. Ryzhikov et al. (1979) reported this species to be a parasite of *Marmota* and the ground squirrels in many localities of the USSR. Contrary to *A. leavis*, the male of the species *A. tarbagan* has no rugose ornamentation around the cloaca.

Schulz (1931) described the species *Ascaris joffi* from *Citellus pigmaeus* in the USSR. This species is known at the present time (only according to the females) from many localities of the USSR not only as a parasite of *C. pigmaeus*, but also *C. suslicus* and *C. fulvus*. It differs in principle from *A. tarbagan* in that the lips have only simple papillae (compare Ryzhikov et al. 1979).

Mozgovoy (1951) presented all species of the genus *Ascaris* parasiting in rodents, with the exception of the species *A. pigmentata*.

Babero (1960) considers the species *A. tarbagan* to be a synonym for the species *A. laevis*.

Sprent (1968) created the genus *Baylisascaris* where he classified the species *Ascaris laevis* Leidy, 1856. An outstanding character distinguishing the genus *Baylisascaris* from the genus Ascaris is the rugose structure around the cloaca of the male, typical for the genus *Baylisascaris*.

Hartwich (1975) does not acknowledge the genus *Baylisascaris* Sprent, 1968. He considers *A. tarbagan* Schulz, 1931 as a synonym for the species *A. laevis* Leidy, 1856. He assumes that the species *A. joffi* Schulz, 1931 and *A. pigmentata* v. Linstow, 1897 could also be synonyms for *A. laevis*.

Ryzhikov et al. (1979) acknowledge the genus *Baylisascaris* Sprent, 1968. As bona species they consider *Baylisascaris laevis* (Leidy, 1856), *Ascaris tarbagan* Schulz, 1931 and *A. joffi* Schulz, 1931. They do not mention the species *A. pigmentata* v. Linstow, 1897.

CONCLUSION

The species *A. tarbagan* Schulz, 1931 was examined using scanning electron microscopy for the first time. It was confirmed that the males are markedly

different from the related species *A. laevis* Leidy, 1856 because males of *A. tarbagan* have no rugose structure around the cloaca. Compared with literary data (see e.g. Tiner 1951) another difference is that on the surface of the eggs there is no net-like structure.

In the species *A. tarbagan*, SEM has also shown the morphology and number of denticles on the lips, the morphology of the lip papillae and the morphology of the surface of the spicules.

Discussions have pointed to various opinions about the value of species of the genus *Ascaris parasiting* in rodents. The authors of the present study agree with those authors who consider the species *A. tarbagan* Schulz, 1931 to be a bona species. They suggest that the name *Ascaris pigmentata* v. Linstow, 1897 be considered as nomen nudum.

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CARABIDS (COL., CARABIDAE) IN THE EPIGEON OF PEST MANAGEMENT APPLE ORCHARDS IN SOUTH BOHEMIA

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A b s t r a c t. In 1985 and 1986, 33 309 adult carabids of 80 species and 30 genera were caught in pitfall traps in four apple orchards (A — unshaded, 5-year-old orchard with grass sod, B and C — shaded 15-year-old herbicide bareground, D — ecological orchard) in South Bohemia (500 m a.s.l.). Species typical of open, unshaded or little shaded biotopes prevailed. Only 18 species occurred in all four orchards, including 6 of the 7 carabids typical of agrocoenoses of Central Europe. The seventh species was found only in orchards A and B. Species diversity was highest in the grassy plots A and D, with a low degree of dominance and relatively high equitability in contrast to the herbicide baregrounds B and especially C. Investigation into the effects of herbicide bareground on the qualitative and quantitative structure of the carabid fauna revealed a substantial decrease in the abundance of individual species (by about 77 % compared with the grassy orchards); diversity was only 9 % lower. The most natural was the structure of carabid community in the ecological orchard. Investigations of possible immigration of eudominant, dominant and subdominant species over soil surface from the environs into the orchards treated with chemicals did not produce any significant results. These species probably survive and reproduce in the orchards. Herbicide bareground is less suitable for the survival and reproduction of carabid beetles than a grassy orchard.

INTRODUCTION

The use of herbicides is a common agricultural practice at the present time. Because of their high effectiveness herbicides are used for destroying weeds as well as eradicting all undesirable vegetation in some cultivated plots, above all orchards, to prevent its competition with young trees for moisture available to roots.

We investigated the effects of bareground in apple orchards on the qualitative and quantitative structure of carabid fauna. We also wanted to find out whether the beetles survived on the herbicide bareground, or whether the piece of land was colonized anew every year.

Carabids as part of the entomofauna of pest management apple orchards have not yet been investigated in Czechoslovakia, contrary to other countries. Most of such studies were made in Canada where H o l l i d a y and H a g l e y (1979) investigated horizontal and vertical distribution of Carabidae in relation to time. They found that density was highest in late summer, with most beetles occurring in the depth to 30 cm. In another study H o l l i d a y and H a g l e y (1984) investigated the effecst of sod type on the abundance and diversity of carabid populations. They found that neither the sod type (*Festuca rubra* L., *Lolium perenne* L.) nor tillage affected the structure and diversity of the fauna, but affected substantially its abundance. Density was highest in a plot with natural sod, lowest in a tilled plot. The abundance of *P. melanarius* on

overgrown and bare ground in an apple orchard in the Federal Republic Germany was investigated by Basedow and Dickler (1981). They found that in both sod types it depended on the type of weather (humidity, temperature) in a given year.

Hagley, Holliday and Barber (1982) studied food structure in the carabid species which are abundant in apple orchards, *Pterostichus melanarius*, *Harpalus aeneus* and *Amara* spp. ate readily young larvae of the codling moth, which means that they may be its potential predators. Loughridge and Luff (1983) investigated food preferences of *Harpalus aeneus* in relation to aphid populations. They found that it is a potential predator of aphids, depending on temperature and their density.

The family Carabidae was also included in comprehensive studies of the arthropodan fauna in apple orchards in Ontario (Hagley, 1974) and California (Altieri and Schmidt, 1985). Research carried out in Hungary, where a team of authors investigated the arthropodan fauna of apple orchards including carabids (Mészáros et al., 1984), was closest to Czechoslovak situation in the geographic and, consequently, the faunistic respect. Kasandrova (1970) reported on the structure of carabid fauna in apple orchards in the Tambov and Ryazan regions of the Soviet Union in relation to the age and spacing of trees.

MATERIAL AND METHODS

Description of the investigated plots

Four apple orchards (A, B, C, D) in the altitude of approximately 500 m in the area of Chelčice (49.08 N, 14.05 E), South Bohemia were investigated in 1985 and 1986 from April to October — November.

Orchard A: 31.36 ha, with young trees planted in 1982. In contrast to soil surface in orchard B, most of which was shaded, the soil surface in orchard A was exposed to sunshine. The apple trees — Spencer, Idared, Spartan and Mustsu — were expected to bear fruit in 1987. The trees were 3 m apart in rows 5 m apart. Grass was regularly mown and left on the ground. Herbicides were applied only near the trees.

Orchard B: 5.14 ha, a herbicide bareground without any vegetation. The trees — Jonathan, Idared and Bláha Orange — were planted in 1971 and spaced as in orchard A. In both years herbicides, fungicides, selective insecticides and fertilizers were applied during the growing season.

Orchards A and B were separated by a 10 m strip of trees (mostly *Quercus robur*, *Fraxinus excelsior*, *Robinia pseudoacacia*), with *Urtica dioica* forming the herb stratum.

Thirty pitfall traps were installed in each orchard, from the buffer strip into the orchard, under apple trees 1, 3, 5, 9, 17 and the last in the row. The same order was applied to rows.

Orchard C: 10.16 ha of herbicide bareground. The trees — Indared, Jonathan, Bláha Orange and Lord Lambourne — were planted in 1970, 3 × 5 m apart, in 1985 they were about 2 m high and bearing fruit. Soil surface was shaded. Fungicides (Rubigan, Venturol, Vegaflor, Sonax, Bayleton, Baycor), herbicides (Aniten combi N, Reglone, Gramoxone, Ustimex, Roundup, Simazin, Zeazin) and insecticides (Zolone EC, Pirimor) were applied in both years of our investigations. Only 9 traps were installed in this orchard, five at its northern edge under the first tree in rows 1, 3, 5, 9 and 17, and four in the first row in the same order, from the edge into the orchard.

Orchard D was situated about 3 km from the village Chelčice, a little higher than the other three (563 m a.s.l.). It was very small, 50 × 40 m (0.2 ha), with natural sod that was not treated with chemicals (we call it ecological orchard in the following text). On two sides it bordered with a field of maize in 1985, which was turned

into a pest management apple orchard in 1986, and with a meadow and a farmhouse on the other two. Trees in this orchard were various cultivars of different ages and heights. We installed only five traps because of the small size of this plot.

Sampling

Material was gathered by the method of pitfall traps. One-litre preserve jars, 15 cm deep, neck 7.3 cm in diameter were let in the ground up to the rim. A small roofs was placed over each jar to protect it from flooding. The traps were filled up to 1/4—1/3 with a 4 % formaldehyde solution and were not baited. The traps were

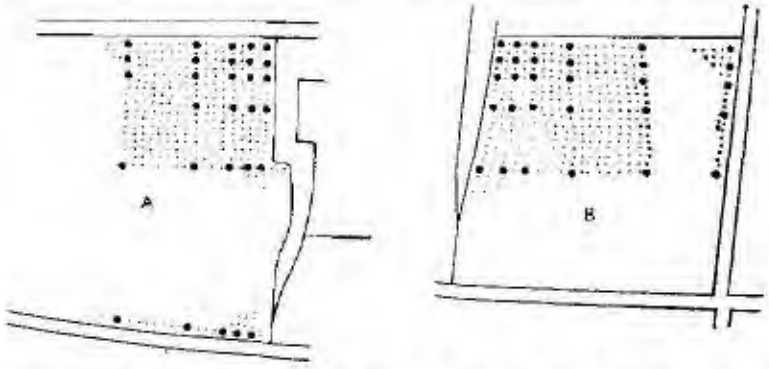

Fig. 1. Spacing of pitfall traps in orchards A and B; trees under which the traps were installed are accentuated.

laid as follows: 30 in orchard A, 30 in orchard B, 9 in orchard C and 5 in orchard D. Three control traps were installed in the 10 m buffer strip between orchards A and B in the second year of this study. For the spacing of the traps see Fig. 1.

Samples were taken nine times in 1985, on 30. 4., 17. 5., 30. 5., 22. 6., 19. 7., 13. 8., 4. 9., 4. 10., 31. 10., and eight times in 1986: 24. 4., 15. 5., 6. 6., 18. 7., 19. 8., 22. 9., 26. 10. and 22. 11. In the two years we collected 33 309 carabids of 80 species and 30 genera.

Tab. 1. Total number of carabid individuals and species captured in pitfall traps in 4 orchards

Plot	No. pitfall traps	1985 Specimens	1985 Species	1986 Specimens	1986 Species	Total Specimens	Total Species
A	30	12 316	62	11 722	53	24 038	66
B	30	2 115	50	3 472	52	5 587	61
C	9	1 402	28	1 277	23	2 679	33
D	5	477	35	528	31	1 005	41
Total	74	16 310	74	16 999	68	33 309	80

Evaluation of the material

Jaccard's and Sørensen's quotiens of similarity (Odum 1977) were used for comparing the four orchards. Simpson index of dominance (C), index of equitability (e) and Shannon-Weaver index of species diversity (H')

(Odum 1977) were used for comparison and characterization of species diversity at the localities. Per cent dominance was evaluated by a five-grade scale: eudominant $\geq$ 10 %, dominant 5 to 10 %, subdominant 2 to 5 %, recedent 1 to 2 %, subrecedent $<$ 1 % (Tischler, 1949).

We investigated the eudominant, dominant and subdominant species for possible immigration into the chemically treated orchards via soil surface, using Kruskal-Wallis nonparametric ANOVA and nonparametric Wilcoxon two-sample test (Sokal and Rohlf, 1981).

For finding out whether carabids preferred the same traps in both years we used Spearman's rank correlation coefficient (Sokal and Rohlf, 1981).

RESULTS

Comprehensive analysis of samples

In total 33 309 adult carabids of 80 species and 30 genera were collected in the four orchards during two years. Data on the number of traps and species and individuals captured at individual localities, in total and in the individual years, are summarized in Table 1. It shows that species diversity was greatest in the grassy orchard A with a minimum of shade. The number of carabid beetles caught there was absolutely as well as relatively largest. Only 9 % species less were found in orchard B, the shaded herbicide bareground. However, significant was a substantially lower (by 77 %) number of individuals caught in the same number of traps. The number of species was lowest in orchard C, the shaded herbicide bareground, but the carabids were more abundant there than in the similar orchard B. Diversity was surprisingly high in the ecological orchard D, considering its very small size.

The number and diversity of carabids at each locality in both years are given in Table 2, and eudominant, dominant and subdominant species in Table 3.

Qualitative analysis of the carabid fauna

Altogether 80 species were found in the four orchards. Surprisingly many species, 18, belonged to the genus *Amara*, 7 to *Carabus* and *Bembidion*, 6 to *Harpalus* and *Pterostichus*, 3 to *Nothiophilus*, *Agonum* and *Abax*, 2 to *Badister*, *Calathus*, *Ophonus*, *Poecilus* and *Trechus*, and 17 genera were represented by one species each.

Two third of the species are characteristic of open or little shaded biotopes with a thin or thick herb stratum. 70 % of them are typical of drier variants of these biotopes. The remaining one third are species living in shrub formations and woods. Consequently, these species as well as hygrophilous carabids of open biotopes occurred primarily in orchards B, C and D where trees were relatively high and the ground was shaded.

The structure of the fauna corresponds to the altitude of about 500 m. Some thermophilous elements *(A. ingenua, N. pusillus, P. bipustulatus, L. depressus)* were mostly found in orchard A, which at the time of our investigation was a grassy southern slope with steppe carabid elements. The character of its fauna is evident in the occurrence of 18 species of *Amara*. Remarkable in faunistic respect is the occurrence of *Amara majuscula* and *Lasiotrechus discus* which are considered rare in Bohemia.

We analysed the carabid fauna of the four orchards by two basic breeding types (Tab. 2) and found that 30 % of the species were of the breeding type with larval diapause and 70 % without it in the annual reproduction cycle.

Tab. 2. Carabid species and specimens captured in four orchard plots

Species	A 1985	A 1986	B 1985	B 1986	C 1985	C 1986	D 1985	D 1986	Breeding type
Abax carinatus (Duft.)	–	–	2	6	–	–	–	1	o
Abax parallelepipedus (Pill. et Mitterp.)	1	–	–	–	–	–	–	2	+
Abax parallelus (Duft.)	–	–	2	3	–	–	3	3	o
Agonum dorsale (Pont.)	3	1	4	4	–	–	–	–	o
Agonum muelleri (Hbst.)	–	1	–	–	–	–	–	–	o
Agonum sexpunctatum (L.)	1	2	1	–	–	–	–	–	o
Amara aenea (De Geer)	44	19	4	1	3	–	1	3	o
Amara apricaria (Payk.)	4	5	–	–	–	–	–	–	d
Amara aulica (Panz.)	2	2	1	1	–	–	–	–	d
Amara bifrons (Gyll.)	2	–	–	–	–	–	–	–	d
Amara communis (Panz.)	42	21	–	3	–	–	5	4	o
Amara consularis (Duft.)	207	44	6	2	–	–	–	1	d
Amara convexior Steph.	2	3	1	1	–	–	5	4	o
Amara eyrinota (Panz.)	4	1	–	1	–	–	–	–	o
Amara familiaris (Duft.)	13	9	5	5	1	2	3	3	o
Amara ingenua (Duft.)	6	39	–	–	–	–	–	–	o
Amara lunicollis Schiødte	1	–	–	–	–	–	1	–	o
Amara majuscula (Chaud.)	2	–	–	–	–	–	–	–	d
Amara montivaga Sturm.	50	67	1	2	3	4	89	58	o
Amara nitida Sturm.	–	1	–	–	1	–	6	3	o
Amara ovata (Fab.)	6	11	1	1	–	–	–	–	o
Amara plebeja (Gyll.)	3	–	6	1	–	–	–	1	o
Amara similata (Gyll.)	16	4	4	1	1	–	–	–	o
Amara tibialis (Payk.)	2	–	–	–	–	–	–	–	o
Anisodactylus binotatus (Fab.)	110	57	6	4	–	–	–	–	o
Asaphidion flavipes (L.)	–	–	–	–	1	–	–	–	o
Badister bipustulatus (Fab.)	5	1	13	4	–	–	1	–	o
Badister lacertosus Sturm.	3	–	–	15	2	–	1	–	o
Bembidion bruxellense Wesm.	–	–	2	–	–	–	–	–	o
Bembidion guttula (Fab.)	–	–	–	1	–	–	–	–	o
Bembidion lampros (Hbst.)	698	526	80	524	16	55	4	15	o
Bembidion nitidulum (Mrsh.)	–	–	2	–	–	–	–	–	o
Bembidion obtusum Serv.	4	18	–	1	–	–	–	–	o
Bembidion quadrimaculatum (L.)	2	–	5	6	–	2	1	1	o
Bembidion tetracolum Say.	–	–	–	2	–	–	–	–	o
Calathus fuscipes (Goez.)	3178	1106	575	522	516	402	24	17	d
Calathus melanocephalus (L.)	221	118	16	25	29	6	11	5	d
Carabus convexus Fab.	63	65	10	10	–	1	5	7	o
Carabus glabratus Payk.	2	–	1	–	–	–	–	–	d
Carabus granulatus L.	142	270	34	73	5	3	2	8	o
Carabus hortensis L.	12	5	14	2	1	1	9	1	d
Carabus nemoralis Müll.	1	1	–	–	–	–	17	19	o
Carabus scheidleri Panz.	–	–	–	–	–	–	1	1	o
Carabus violaceus L.	37	88	21	10	–	–	1	3	d
Clivina fossor (L.)	10	3	–	2	1	–	–	–	o
Dromius notatus Steph.	–	–	1	1	–	–	–	–	o
Harpalus aeneus (Fab.)	299	286	46	94	26	10	2	–	o
Harpalus honestus (Duft.)	33	45	–	5	–	–	–	–	o
Harpalus latus (L.)	8	6	–	3	–	–	2	3	o
Harpalus rubripes (Duft.)	2	2	–	–	–	1	–	–	o
Harpalus rufitarsis (Duft.)	6	1	–	–	–	–	–	1	o

cont.

Species	A		B		C		D		Breeding type
	1985	1986	1985	1986	1985	1986	1985	1986	
Harpalus tardus (Panz.)	75	177	9	21	–	–	–	–	o
Laemostenus discus (Fab.)	3	–	–	–	–	–	–	–	d
Lebia chlorocephala (Hoff., Koch., P. Müll., Linz.)	–	–	1	–	–	–	–	–	o
Licinus ferrugineus (L.)	4	1	4	–	1	–	–	–	d
Licinus depressus (Payk.)	–	–	–	–	–	1	–	–	o
Loricera pilicornis (Fab.)	137	15	5	4	1	–	–	–	o
Microlestes minutulus (Goez.)	3	1	1	–	1	–	–	1	o
Nebria brevicollis (Fab.)	31	3	68	54	164	89	–	–	d
Nothiophilus biguttatus (Fab.)	1	1	27	32	12	20	–	–	o
Nothiophilus palustris (Duft.)	2	1	4	11	–	–	4	2	o
Nothiophilus pusillus Waterh.	4	–	3	1	–	–	1	–	o
Ophonus punctatulus (Duft.)	–	–	–	1	–	–	–	–	d
Ophonus rufibarbis (Fab.)	1	–	1	–	–	–	–	–	d
Panagaeus bipustulatus (Fab.)	1	–	–	3	–	–	–	–	o
Platynus assimilis (Payk.)	–	–	8	7	1	–	11	1	o
Poecilus cupreus (L.)	922	2164	22	69	3	4	4	2	o
Poecilus versicolor Sturm.	828	2600	7	18	13	13	148	287	o
Pseudoophonus rufipes (De Geer)	3221	1694	127	426	6	6	3	10	d
Pterostichus melanarius (Ill.)	1715	2127	887	1415	576	662	99	49	d
Pterostichus niger (Schall.)	40	57	29	32	5	5	7	12	d
Pterostichus nigrita (Fab.)	–	2	–	–	–	–	–	–	o
Pterostichus oblongopunctatus (Fab.)	5	2	1	–	1	1	1	1	o
Pterostichus strenuus (Panz.)	7	27	4	21	–	–	–	–	o
Pterostichus vernalis (Panz.)	3	10	1	5	2	6	–	–	o
Stomis pumicatus (Panz.)	–	1	1	2	–	–	1	–	o
Syntomus truncatellus (L.)	–	–	–	–	–	–	2	–	o
Synuchus nivalis (Panz.)	22	7	2	1	–	–	1	–	d
Trechus quadristriatus (Schrk.)	43	1	39	13	10	1	1	–	d
Trechus secalis (Payk.)	1	3	–	–	–	2	–	–	d
Total	12 316	11 722	2115	3472	1402	1277	477	628	
No. species	62	53	50	52	28	23	35	31	

o – without larval diapause, d – with larval diapause, + – unstable development

These proportions correspond with the structure of carabid fauna of open, unshaded or little shaded biotopes in Central Europe.

Comparison of the four orchards showed that of the 80 species only 18 occured at all four localities (Tab. 4). With the exception of *Amara montivaga*, which is typical of unshaded grassy vegetation in hilly and submontane areas, all these species range with the most abundant representatives of the family in Bohemia. Species inhabiting open, unshaded biotopes prevailed (*A. aenea, B. lampros, C. fuscipes, H. aeneus, P. cupreus, P. versicolor*) along with typical forest species (*C. hortensis, P. oblongopunctatus*) whose presence in the orchards suggested that forest was the original biotope. Among the 18 species found in the four orchards there were 6 of the 7 carabids typical of Central European agrocoenoses (Jarošík and Hůrka, 1986); the seventh species, *Agonum dorsale*, was found only in orchards A and B.

Tab. 3. Per cent dominance of carabid species in four orchard plots

Plot	1985			1986		
A	*Pseudoophonus rufipes*	26.2	ED	*Poecilus versicolor*	22.3	ED
	Calathus fuscipes	25.8	ED	*Poecilus cupreus*	18.6	ED
	Pterostichus melanarius	13.9	ED	*Pterostichus melanarius*	18.2	ED
	Poecilus cupreus	7.5	D	*Pseudoophonus rufipes*	14.5	ED
	Poecilus versicolor	6.7	D	*Calathus fuscipes*	9.4	D
	Bembidion lampros	5.7	D	*Bembidion lampros*	4.5	SD
	Harpalus aeneus	2.4	SD	*Harpalus aeneus*	2.4	SD
	3 R and 52 SR	11.8		*Carabus granulatus*	2.3	SD
				2 R and 43 SR	8.0	
B	*Pterostichus melanarius*	41.9	ED	*Pterostichus melanarius*	40.8	ED
	Calathus fuscipes	27.2	ED	*Bembidion lampros*	15.1	ED
	Pseudoophonus rufipes	6.0	D	*Calathus fuscipes*	15.0	ED
	Bembidion lampros	3.8	SD	*Pseudoophonus rufipes*	12.3	ED
	Nebria brevicollis	3.2	SD	*Harpalus aeneus*	2.7	SD
	Harpalus aeneus	2.2	SD	*Carabus granulatus*	2.1	SD
	6 R and 38 SR	15.7		2 R and 44 SR	12.0	
C	*Pterostichus melanarius*	41.1	ED	*Pterostichus melanarius*	51.8	ED
	Calathus fuscipes	36.8	ED	*Calathus fuscipes*	31.5	ED
	Nebria brevicollis	11.7	ED	*Nebria brevicollis*	5.4	D
	Calathus melanocephalus	2.1	SD	*Bembidion lampros*	4.3	SD
	2 R and 22 SR	8.3		2 R and 17 SR	7.0	
D	*Poecilus versicolor*	31.0	ED	*Poecilus versicolor*	54.4	ED
	Pterostichus melanarius	20.8	ED	*Amara montivaga*	11.0	ED
	Amara montivaga	18.7	ED	*Pterostichus melanarius*	9.3	D
	Calathus fuscipes	5.0	D	*Carabus nemoralis*	3.6	SD
	Carabus nemoralis	3.6	SD	*Calathus fuscipes*	3.2	SD
	Calathus melanocephalus	2.3	SD	*Bembidion lampros*	2.8	SD
	Platynus assimilis	2.3	SD	*Pterostichus niger*	2.3	SD
	6 R and 22 SR	16.3		3 R and 21 SR	13.4	

As concerns the proportion of abundant heliophilous species *Poecilus cupreus* and *P. versicolor*, the former preferring lowlands and hilly areas, the latter submontane areas and mountains, *P. versicolor* was slightly predominant in orchard A and prevailed markedly in orchard D whose altitute is 50 m higher.

Comparison of the orchards

Fig. 2 shows that the four orchards differed considerably in the abundance of carabids. The number of beetles per trap was highest in orchard A (about 400). In orchard C there were 150 beetles trap, in orchard B we found a substantial difference between the two years: 70 carabids trap in 1985 and 115/ /trap in 1986 (the average for both years was 93). Abundance was stable in orchard D with the average of 100 carabids trap.

For comparing the orchards we used the ecological indices given in Methods. Tables 5 and 6 show a great similarity between orchards A and B, less pronounced between A—D and B—D, and slight between A—C, B—C and C—D where the degree of similarity was approximately the same.

Tab. 4. Carabid species found in all four orchards

Species	Plot A	B	C	D
Pterostichus melanarius	ED	ED	ED	ED
Calathus fuscipes	ED	ED	ED	SD
Poecilus vericolor	ED	SR	R	ED
Pseudophonus rufipes	ED	D	SR	R
Bembidion lampros	D	D	SD	R
Poecilus cupreus	ED	R	SR	SR
Harpalus aeneus	SD	SD	R	SR
Amara montivaga	SR	SR	SR	ED
Carabus granulatus	R	R	SR	R
Calathus melanocephalus	R	SR	R	R
Pterostichus niger	SR	R	SR	R
Trechus quadristriatus	SR	R	SR	R
Carabus convexus	SR	SR	SR	R
Amara familiaris	SR	SR	SR	R
Carabus hortensis	SR	SR	SR	R
Amara aenea	SR	SR	SR	SR
Bembidion quadrimaculatum	SR	SR	SR	SR
Pterostichus oblongopunctatus	SR	SR	SR	SR

ED – eudominant, D – dominant, SD – subdominant, R – recedent, SR – subrecedent

Other comparisons showed that the index of species diversity was highest in plots A and D where, consequently, the degree of dominance was low and equitability relatively high. On the contrary, in the herbicide baregrounds B and especially C diversity was lower, the values calculated for orchard B being

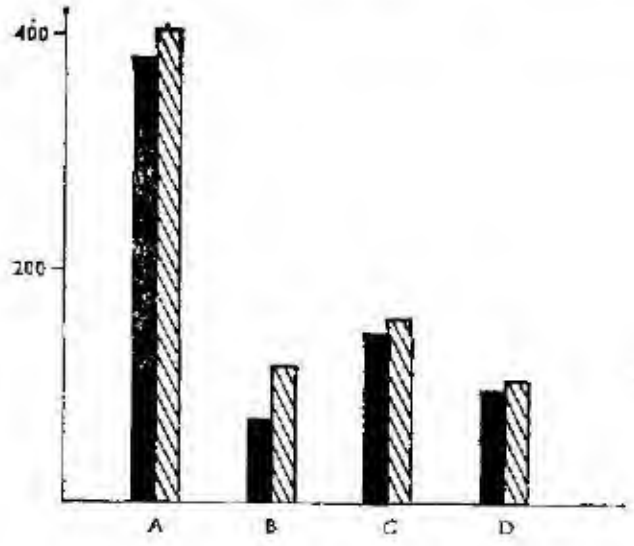

Fig. 2. Total number of carabids per trap in the individual orchards

somewhat closer to A. Plot C was conspicuous by its high degree of dominance and a less balanced representation of species. This is documented by data on the percentage of dominance in Tab. 2.

Immigration

Herbicide baregrounds affect above all the quantitative structure of carabid communities. Therefore, we tried to find out whether carabids can survive in such plots, or whether they immigrate from the vicinity. Our observations were limited to species which cannot fly.

Tab. 5. Jaccard's (Ja) and Sorensen's (Qs) quotient of similarity of carabid communities in four orchard plots

Quotient of similarity	plot A–B	A–C	B–C	A–D	B–D	C–D
Ja	67.10	43.48	42.42	50.70	50.00	42.30
Qs	0.81	0.61	0.59	0.67	0.67	0.59

We concentrated on orchard B, herbicide bareground, using Kruskal-Walis nonparametric ANOVA for assessment of the immigration of carabids into the orchard. We tested dispersal from the south and west by means of series of traps in each row. Three control traps were laid in the buffer strip between orchards A and B in the second year of investigation. Species found in this habitat are given in Tab. 7 which shows that the most abundant species were

Tab. 6. Species diversity (H'), equitability (e) and dominance (c) of carabid communities in different orchard plots

Index	1985 A	B	C	D	1986 A	B	C	D
H'	1.0348	0.8199	0.8426	0.9790	0.8597	0.8713	0.5898	1.4380
e	0.5773	0.4802	0.4444	0.6291	0.4986	0.5077	0.4331	0.9716
c	0.2411	0.2587	0.7257	0.1837	0.4686	0.2295	0.5738	0.3513

Pseudoophonus rufipes, *Pterostichus oblongopunctatus* and *Carabus hortensis*. There was no statistically significant difference among catches in the individual series in either direction. Orchard A was tested in the same way and with the same results. It follows that there was no statistically significant immigration into these orchards over soil surface. However, we must take into account the remnant of wood between plots A and B as a source of the more euryoecious forest species *Pterostichus oblongopunctatus* and *Carabus hortensis*, which were eudominant in this habitat and occurred as subrecedent in both orchards. The stenoecious forest species *H. quadripunctatus* which was dominant in the remnant of wood was not found in either orchard.

Tab. 7. Carabid species occurring in strip of wood 10 m wide (sampled with 3 pitfall traps), comparision with A and B

Species	%	dominance	A	B
Pseudoophonus rufipes	30.4	ED	ED	D
Pterostichus oblongopunctatus	16.5	ED	SR	SR
Carabus hortensis	13.4	ED	SR	SR
Harpalus quadripunctatus	8.8	D	–	–
Calathus fuscipes	8.2	D	ED	ED
Nothiophilus biguttatus	4.1	SD	SR	R
Poecilus versicolor	3.1	SD	ED	SR
Carabus granulatus	2.1	SD	R	R
Bembidion lampros	2.1	SD	D	D
Harpalus tardus		R	R	SR
Abax parallelepipedus		R	SR	
Carabus convexus		R	SR	SR
Pterostichus melanarius		R	ED	ED
Calathus melanocephalus		R	R	SR
Poecilus cupreus		R	ED	R
Dromius quadrimaculatus		SR	–	–
Pterostichus strenuus		SR	SR	SR
Stomis pumicatus		SR	SR	SR
Synuchus nivalis		SR	SR	SR
Nothiophilus palustris		SR	SR	SR
Isodister laeviusus		SR	SR	SR
Amara aenea		SR	SR	SR
Amara similata		SR	SR	SR

ED – eudominant, D – dominant, SD – subdominant, R – recedent, SR – subrecedent

Immigration was investigated in orchadr C too. We tested two sets by Wilcoxon's test of 2 independent samples. The result was the same as in plots A and B, only in 1986 a difference between the two sets at a 90 % level of significance was ascertained in *Calathus fuscipes*. However, we must point out again that only species moving over the soil surface could be recorded.

In connection with the immigration of carabids into the orchards we also tested whether they preferred some of the traps in the two years, using Spearman's rank correlation coefficient (Sokal and Rohlf, 1981). The result was negative, corresponding with the results of Kruskal-Walis's and Wilcoxon's tests, so that dispersal was not confirmed in this way either.

Aspects

The growing season can be divided into several phases, each of them characterized by a somewhat different quantitative and qualitative faunal structure. They are termed aspects. In orchards we can distinguish the spring aspect when grass germinates and grows and trees blossom; it lasts till about the end of June. The summer aspect follows, lasting till the end of August or mid-September. The next aspect is autumnal, with fruit getting ripe.

Species of the developmental type without larval diapause prevail in the spring aspect. Species diversity was much greater in the grassy orchards than on bareground. *Bembidion lampros*, *Poecilus cupreus* and *P. versicolor* were

absolutely predominant in orchard A, *Amara montivaga* and *P. versicolor* in D. Only *B. lampros* occurred in noticeable numbers on the herbicide bare-ground of orchards B and C.

There was not much difference among the four orchards during the summer aspect; *Pterostichus melanarius* and *Pseudoophonus rufipes* were abundant in all. These species belong to the developmental type including larval diapause,

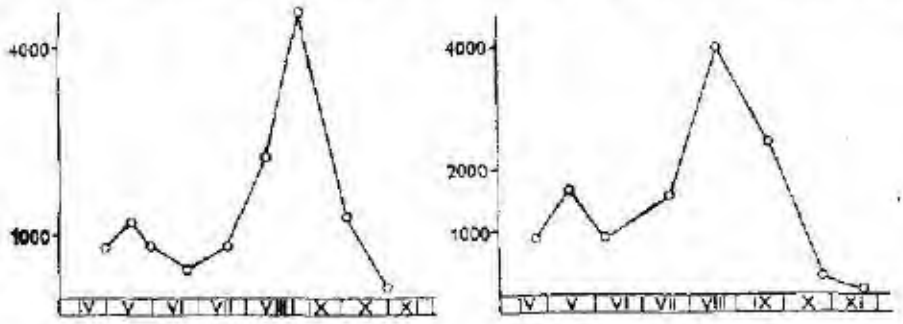

Fig. 3. Movement activity of carabids in orchard A in seasons 1985 and 1986.

but they begin to reproduce already at the end of spring because the gonads of adults do not undergo diapause. The number of adults reaches maximum in summer (Figs. 3, 4), which is in keeping with data from Canada and Europe.

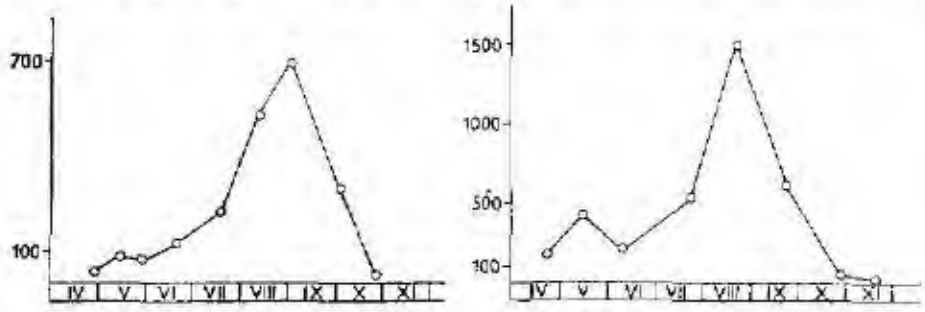

Fig. 4. Movement activity of carabids in orchard B in seasons 1985 and 1986.

Calathus fuscipes prevailed from the beginning of September to the end of November. On the herbicide baregrounds it occurred along with *Nebria brevicollis*. These two species also belong to the developmental type with larval diapause, to the variant including the imaginal diapause of gonads. No dominant representative of the autumnal aspect was found in orchard D. The number of individuals (or their locomotor activity) was rapidly decreasing.

DISCUSSION

In commercial apple orchards of the farming cooperative Mír Chelčice we found relatively many (80) species of carabids. Mészáros et al. (1984) carri-

ed out a similar study in Hungary: for five years they studied the structure of arthropodan fauna in 5 apple orchards, most of which were chemically treated (sprayed up to 20 times a year, including 7—11 treatments with insecticides). Chemicals were not applied to only one control plot. The Hungarian team found 79 species. Considering that Hungary is a warmer country with Mediterrancan elements the number of species found in the South Bohemian orchards is remarkable. K a s a n d r o v a (1970) reported 63 species from Tambov and Ryazan regions of the USSR. H a g l e y (1974) found repeatedly only about 40 species in untreated apple orchards in Ontario.

Comparing the carabid faunas of the Hungarian and South Bohemian orchards we find that 33 species occur there in both countries. The Czech eudominant, dominant and subdominant species *Bembidion lampros, Calathus fuscipes, Calathus melanocephalus, Harpalus aeneus, Pseudoophonus rufipes, Poecilus cupreus, Poecilus versicolor, Pterostichus melanarius* and *Pterostichus niger* live in Hungarian orchards too. Analyses of carabid fauna sampled by light trapping in apple orchards (Hungary — K á d á r, S z e n t k i r á l y i, 1983; Federal Republic Germany — B a s e d o w and D i e k l e r, 1981) revealed sets of carabid species flying into the orchards from the vicinity rather than the fauna of the orchards.

The qualitative structure of the carabid community of apple orchards resembles by its most abundant species carabid communities of various agrocoenoses (potato fields, hop gardens, fields of beet, corn, etc.). J a r o š í k and H ů r k a (1986) found that the biocoenoses of all these crops in Czechoslovakia include 7 carabid species which may be subdominant, dominant or eudominant. They are *Agonum dorsale, Bembidion lampros, Calathus fuscipes, Harpalus aeneus, Poecilus cupreus, Pseudoophonus rufipes* and *Pterostichus melanarius*. With the exception of *A. dorsale* their dominance in the apple orchards exceeded 2 %. Intensive management apple orchards can then be regarded as agrocoenoses because of the structure of their carabid fauna. K a s a n d r o v a (1970) pointed this out, too.

Our experimental plots differed above all in the quantitative representation of individual species. Comparison of the total numbers of individuals at the two main localities A and B shows a considerable difference, because the number in orchard B is lower by about 77 %. Apparently, for most carabids the grassy orchard A was ecologically preferable to the bareground B. The absence of vegetational cover affects in turn all stages of the trophic pyramid up to predators. Because the grass in orchard A was regularly mown at about 14-day intervals and was left on the ground the beetles had shelter at daytime when most of them were inactive. The Canadian (H o l l i d a y and H a g l e y, 1984) and American (A l t i e r i and S c h m i d t, 1985) authors also found a marked difference in the number of carabids in orchards with and without undergrowth.

The numbers of individuals caught in orchards A and B (Figs. 3 and 4) indicate that the applied chemicals directly affect carabids, above all during their development (decrease in June). J a w o r s k a (1981) arrived at similar conclusions on finding that application of Mesoramil and Semeron to cabbage fields reduced the abundance of carabid species with spring activity.

The average number of individuals per trap in orchard D was one of the lowest (Fig. 2) although the plot was never treated chemically and was therefore the most suitable from the ecological point of view. The samples may

have been so small because of the grassy undergrowth that was thick throughout the growing season, impeding the movement of carabids and thus reducing the effectiveness of the traps.

The difference between the two years of research in the numbers of captured individuals was very small. In 1986 we found almost 4 % more individuals, but 8.5 % fewer species, most of them subrecedent.

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UNUSUAL KARYOTYPES IN APODEMUS CF. FLAVICOLLIS AND MICROTUS AGRESTIS (MAMMALIA, RODENTIA)

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A b s t r a c t. Heterozygous chromosome rearrangements, which can be explained by Robertsonian mechanisms, were found in two specimens of free-living rodents — *Apodemus* cf. *flavicollis* and *Microtus agrestis*. Two small autosomes of approximately the same size were involved in a presumptive centric fusion observed in a male of *Microtus agrestis*. Two chromosomes of distinctly different size were fused in a female of *Apodemus* cf. *flavicollis*. A small dot-like chromosome fragment was regularly present in cells carrying the rearrangement. Simultaneously with the cells possessing the rearrangement, cells with a normal karyotype were observed in the bone marrow of the specimen. The karyotype variants in both specimens probably originated after new mutations.

Findings of karyotypes presumed to have evolved as a consequence of mutations originating de novo are very rare in populations of free-living mammals (e.g., F r e d g a 1968, L' a p u n o v a and K a r t a v c e v a 1976, T h a l e r 1978, Z i m a and K r á l 1982). The probable cause of this rarity is primarily the low mutation rate of chromosome changes as well as the negative selection pressure usually operating against the new rearrangement carriers. The latter factor is especially important in the case of unbalanced rearrangements, and/or in changes with a deleterious effect manifested by decreased vitality or fertility.

Herein we report abnormal karyotypes observed in two specimens of small rodents captured in free nature. Similar rearrangements have not yet been found in many hundreds of specimens of those species. Therefore, we suggest these two karyotypes to be a result of new mutations.

MATERIAL AND METHODS

A karyotypically abnormal specimen belonging to the genus *Apodemus* was trapped on July 9, 1986, in the locality Skalní mlýn situated in the Moravian Karst (49°20′ N; 16°45′ E). The specimen appeared to be a young female (weight 7 grams, body length 62 mm, tail length 60 mm, hind foot length 21,5 mm, auricle length 15 mm). The sexual organs of the female were inactive and intact. Due to somatic immaturity, it was not possible to exclude, without doubt, the specific pertinence of the animal to *Apodemus sylvaticus*. Nevertheless, on morphological grounds and with respect to the ecological circumstances of the capture, we are inclined to believe that the specimen studied belongs to *Apodemus flavicollis*.

A specimen of the field vole (*Microtus agrestis*) with an abnormal karyotype was trapped on July 1, 1982, in the Siedmich prameňov Valley in the Belianské Tatra Mts. (49°15′ N; 20°10′ E). The specimen was a mature and sexually active male (weight 38 grams, body length 106 mm, tail length 35 mm, hind foot length 18 mm, auricle length 13 mm). The size of the testes averaged 13 × 7 mm.

Table 1. Karyotypes ascertained in the bone marrow cells of the *Apodemus* specimen

karyotype characteristics	no. of metaphases found	%
2n = 50, large submetacentric and dot-like fragment	41	70.7
2n = 49, large submetacentric and dot-like fragment	5	8.6
2n = 48, large submetacentric and dot-like fragment	1	1.7
2n = 50, large submetacentric	1	1.7
2n = 49, large submetacentric	1	1.7
2n = 50, acrocentric chromosomes only	9	15.5
total	58	

Slides of somatic chromosomes of both specimens were prepared in the field using the direct bone marrow technique described by Ford and Hamerton (1956). Only conventionally stained chromosomes were studied and no banded karyotypes of sufficient quality were obtained.

The skulls and skins of both specimens are deposited in the collections of the Institute of Systematic and Ecological Biology, CAS, in Brno.

Table 2. Chromosome numbers found in the bone marrow cells of the *Microtus agrestis* specimen

	no. of chromosomes						total
	45	46	47	48	49	50	
no. of metaphases found	1	2	2	11	38	1	55
%	1.8	3.6	3.6	20.0	69.1	1.8	

RESULTS

Apodemus cf. *flavicollis* (Plate I a, b)*

50 chromosomes were found in most of the cells of the specimen from the Moravian Karst examined. The most frequently observed cells contained 48 acrocentric chromosomes, one odd large submetacentric chromosome, and one very small, dot-like fragment. The large submetacentric chromosome and the dot-like fragment were also found in several cells with 48, and 49 chromosomes. Two cells with 49 and 50 chromosomes contained only the large submetacentric, and the dot-like fragment was missing. In some of the cells studied, only 50 acrocentric chromosomes were ascertained. The large submetacentric chromosome as well as the dot-like fragment were never observed in these 50 acrocentric chromosome cells. A synopsis of the quantitative distribution of various karyotypes in the sample of the bone marrow cells studied is presented in Table 1.

*Plate I will be found at the end of this issue.

These observations may be explained as a mosaic occurrence of two cells lines in bone marrow. Some of the cells contained a normal chromosome set with 48 acrocentrics and, in addition, with two supernumerary (B-) elements. The occurrence of supernumerary chromosomes is rather frequent in *Apodemus flavicollis* populations inhabiting the geographical region concerned. The other presumed cell line, occurring in the sample examined more frequently, had a karyotype containing a Robertsonian fusion of two chromosomes. The large submetacentric and the dot-like chromosome fragment presumably appeared as a consequence of this fusion. The other karyotypes may be considered as artifacts originating after individual chromosome losses during preparation.

Microtus agrestis (Plate I c)

44 acrocentric autosomes, an odd medium-sized metacentric, two small metacentric autosomes, and ordinary large sex chromosomes X and Y were ascertained in the bone marrow cells of the specimen captured in the Belianské Tatra Mts. The numbers of chromosomes found in the cell sample examined are presented in Table 2. The medium-sized metacentric was observed in all cells studied. The ascertained number of aneuploid cells did not exceed the proportion usually found in slides prepared by the direct treatment of bone marrow cells. We can conclude that the bone marrow cells of the specimen studied contained a Robertsonian fusion of two autosomes of similar size, resulting in the reduction of the chromosome number (2n = 49).

DISCUSSION

The intraspecific occurrence of Robertsonian fusion within the genus *Apodemus* is known only in the Japanese species, *A. speciosus* (Shimba and Kobayashi 1969, Tsuchiya 1979). This species is characterized by the presence of two parapatrically distributed karyotypic races differing in a single Robertsonian rearrangement. In the genus *Microtus*, several cases of intraspecific Robertsonian karyotype variation have been described (Kovalskaja 1977, Fredga et al. 1980).

The karyotypes reported in this study are quite unique, and comparable changes have not been described in any of the species concerned. In our laboratory, we have examined the karyotype in 457 specimens of the genus *Apodemus*, including 412 specimens of *A. flavicollis* and *A. sylvaticus*. 44 specimens of these species were karyotypically studied in the locality of Skalní mlýn. We have investigated karyotypes of 72 specimens of *Microtus agrestis*, including 19 specimens captured in the Siedmich prameňov Valley in the Belianské Tatra Mts. A large number of specimens belonging to these rodent species was karyologically studied by various authors in different geographical regions (see Zima and Král 1984 for a review) but the occurrence of any Robertsonian rearrangement has never been reported. We suggest, therefore, that the rearrangements observed are not involved in a population polymorphism, but that they are products of new mutations. A somatic chromosome rearrangement in the specimen belonging to the genus *Apodemus*, and a germ cell chromosome rearrangement in the specimen of *Microtus agrestis*, are presumptive causes of the origin of the abnormal karyotypes.

The mosaic occurrence of a Robertsonian change in the bone marrow cells of a specimen of *Apodemus* cf. *flavicollis* brings an interesting proof of the mechanism of this type of rearrangement. A presumptive origin of an acentric

or centric chromosome fragment is supposed to result from Robertsonian fusions occurring through a classical translocation mechanism (John and Freeman 1975, Schulz-Schaeffer 1980). A rapid elimination of such a fragment can be expected because of its mitotic and meiotic instability, and evidence of its existence is therefore usually not available. Centric fragments have been found in human karyotypes (Hoehn et al. 1970) but in the cases described, the direct relationship of their presence to a Robertsonian fusion was not established. The finding described in the specimen of *Apodemus* cf. *flavicollis* represents probably the first empirical evidence of the actual occurrence of these translocation products.

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ON THE GROWTH RATE OF BROWN TROUT (SALMO TRUTTA M. FARIO) IN SOME BULGARIAN RIVERS AND METHODS FOR ITS STUDY

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A b s t r a c t. Studied is the growth rate of river trout in 26 rivers in Bulgaria, compared to that of 120 rivers from its entire range. The obtained results are given in mean values broken down according to drainage basins. Discussed and employed are more precise and easier ways for back calculations of length and weight, comparative analysis of growth and calculation of the coefficient of condition. A critical analysis is presented of the biological sense of the parameters of the equation of Bertalanffy.

INTRODUCTION

Brown trout (*Salmo trutta* m. *fario* L.) is the dominant and often only species inhabiting trout river in Bulgaria. In spite of this there are few data on its growth (B e l č e v a, 1959; D i k o v and J a n k o v, 1985; J a n k o v 1986).

The data presented here were collected from six river systems in Bulgaria from 1978 to 1982 year.

MATERIALS AND METHODS

The material was gathered during the summer and autumn from 26 rivers from the drainage areas of the Vacha, Chaya, Mesta, Struma, Iskar and Vit rivers, at an average elevation a.s.l. above 800 m (500—1450 m) and with gradient mostly above 28 ‰. The river beds were usually covered with gravel and large stones. The rivers are from 3 to 10 m width, 10—40 cm deep and pools were up to 60—80 cm deep. Oxygen content of the water is above 8 mg l^{-1}, pH — 8.5 to 8.8, total hardness — 1.0 to 12.6 dH°, oxidability — between 1.8 to 2.5 mg O_2 l^{-1}. Mean annual temperatures vary in different rivers between 4 and 8 °C, minimal 0 °C and maximum 18 °C.

Fish were caught by electric fishing using D. C. Generator. A total of 3208 specimens were processed. Measured were standard length (l), Fork length (F.L.) and body length (L). The following correlations were drawn: $L = F.L. \times 1.03$; $L = l \times 1.13$ and $F.L. = l \times 1.09$. All data on body length refers of Fork length, which for short is given as L. The age was established by the scales, taken from the region above the anal fin and above the lateral line. A Dokumator, Lesegerät (Carl Zeiss, Jena, DDR) was used to establish the age, at a magnification of 21 times. The oral radii of the scales (R) were measured.

Owing to great age differences in the growth of L as related to R (Fig. 1), a method was used for the measurement of the growth rate through back calculations (by Ž i v k o v, 1980). The method was as follows: mean values of R are grouped in a manner shown on Table 1. The separate equations of the relations between L and R for each age group (or for several age groups taken together, in cases when there were few specimens (Table 2). After that the values of R_i from Table 1 were used for the calculation of the values of L_i through the successive substitution in the

formula for the first age group: the values of R_2 — for the calculation of the values of L_2 by formula for the second age group and so on. The values of L_1, L_2 and so on are given as mean values for the whole population.

The values of W were calculated in an analogous way through L. To this purpose

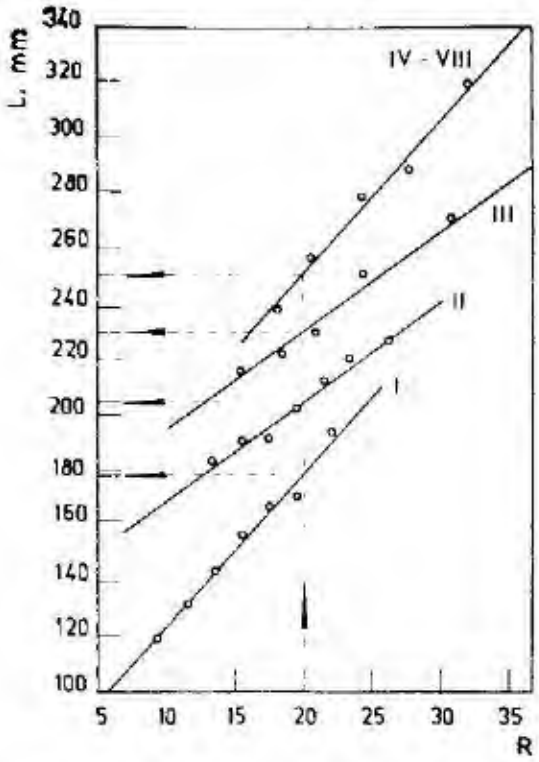

Fig. 1. Relationship between body length (L, mm) and oral radius of scale (R, in parts of the micrometer eye-piece) in different age groups (I, II . . .) of brown trout in the Vacha drainage basin. At one and the same value of R (for instance 20) values of L in different groups are very variable (dotted lines).

Table 1. Grouping of average values of annual scale rings (R) and the corresponding back-calculated body lengths (L) values

Generation	Age group	Average values of R and L at various ages										Number of specimens
		1		2		3		4		5		
1987	I	R_1	L_1									n
1986	II	R_1	L_1	R_2	L_2							n
1985	III	R_1	L_1	R_2	L_2	R_3	L_3					n
1984	IV	R_1	L_1	R_2	L_2	R_3	L_3	R_4	L_4			n
1983	V	R_1	L_1	R_2	L_2	R_3	L_3	R_4	L_4	R_5	L_5	n
.	.	.	.	.	.	.	.	.	.	.	.	
.	.	.	.	.	.	.	.	.	.	.	.	.

Table 2. Age and population changes of parameters of equations $L = a + bR$ and $L = a + bR + cR^2$ (L — body length, mm; R — radius of scale, parts of the micrometer eye piece)

drainage basin	age groups 1+ a	b	r	n	2+ a	b	r	n	3+ a
Chaya	31.438	8.376	0.97	58	151.178	2.348	0.97	30	110.047
Vacha	67.925	5.587	0.98	362	132.682	3.597	0.97	257	157.959
Iskar	83.418	3.890	0.94	104	115.470	3.867	0.95	34	
Mesta	68.811	4.177	0.98	352	137.561	1.781	0.84	271	140.503
Struma	60.855	5.735	0.99	387	114.739	3.073	0.96	260	97.964
Vit	39.902	6.233	0.99	294	57.411	5.638	0.99	283	99.194

equations for W-L correlations were drawn up for each age group (Table 3). Coefficient k in these equations ($W = kL^n$) was used directly as a coefficient of condition.

The parameters of the von Bertalanffy equation for linear and weight growth were computed after the method of Hohendorf (1966).

RESULTS AND DISCUSSION

The regression analysis of the relationship between L and R clearly outline age differences in the increment of L as related to R. Fig. 1 clearly illustrates the fact that within one and the same population, at one and the same value of R the values of L in different groups vary considerably. For instance at a mean value of R = 20 parts of the micrometer eye-piece, the value of L for the first age group was only 179 mm, for the second — 205 mm, for the third — 231 mm, while for the fourth to the eight, taken together, 251 mm, i.e. the difference was up to 72 mm. In other words older fish have considerably less scales. However, if we calculate L according to the classical method, (R = 20 parts), by means of the formula valid for the entire Vacha drainage basin, (Table 2), we obtain L = 205 mm.

These results are the most convincing examples in support of our view (Živkov, 1980) that not taking age differences into consideration in the growth of L as related to R could in some cases lead to considerable errors in back calculations of L after R.

Table 3. Age and population changes of parameters of equation $W = kL^b$ ($\log W = \log k + n \log L$) (W — weight, g; L — body length, mm)

drainage basin	age groups 1+ logk	$k.10^{-6}$	n	r	2+ logk	$k.10^{-6}$	n	r	3+ logk
Chaya	−4.818	1.52	2.937	0.998	−5.162	0.69	3.100	0.989	−5.157
Vacha	−4.742	1.81	2.919	0.998	−3.886	13.00	2.557	0.995	−4.669
Iskar	−5.163	0.69	3.082	0.996	−5.081	0.83	3.063	0.997	
Mesta	−5.108	0.78	3.078	0.989	−4.238	5.78	2.693	0.996	−3.437
Struma	−5.149	0.71	3.093	0.998	−4.866	1.36	2.960	0.997	−4.213
Vit	−5.307	0.05	3.039	0.992	−4.862	1.37	2.980	0.989	−4.575

age groups											
3+				(4+) — (8+)				Total			n
b	r	n	a	b	r	n	a	b	c	r	
6.629	0.99	13					8.936	10.397		0.996	101
3.636	0.95	106	139.631	5.553	0.99	58	39.442	8.287		0.997	783
							127.846	−2.186	0.216	0.989	138
2.997	0.94	82	81.245	6.329	0.92	28	58.704	3.936	0.101	0.995	713
5.525	0.95	97	104.920	6.586	0.94	25	89.033	0.236	0.284	0.992	769
4.243	0.97	112	66.323	6.365	0.74	15	30.198	7.106		0.997	704

The mean values of linear increment of river trout from various drainage areas are given in Table 4. Here the growth rate values of the populations (drainage areas) are arranged in descending order on the basis of last value of L in the respective population, i.e., on the basis of the mean values of absolute annual increments (with two neighbouring populations at different ages the classification included only both values of L of the last year of the younger population. Živkov, 1972). It is evident from the table that trout from the Chaya and Vacha drainage areas has the highest growth rate, and that of the Vit river, the lowest. For instance L_5 of trout from the Chaya drainage area is 289 mm, while for trout from the Vit drainage area only 225 mm. Trout from the drainage areas of the Iskar and Mesta are almost identical. An increase of age in the population coincides with a tendency towards a fall in the annual increment (t). Usually the greatest fall in the reduction of the values of t is observed between the first and second, and second and third year, one of the reasons being the sexual maturity of trout which falls in this period.

The comparatively higher growth rate of trout in the Chaya and Vacha rivers can be attributed according to the generally greater hardness of the water of these drainage areas (4.2—12.6 dH°). In the remaining rivers it is considerably lower (1.0—4.2 dH°). Frost and Brown (1973) offer a similar observation on the effect of water hardness on trout growth rate. Also the waters of the Vacha river are characterized by stable oligosaproby (Rous-

age groups										
3+				(4+) — (8+)				Total		
k.10⁻⁵	n	r	logk	k.10⁻⁵	n	r	logk	k.10⁻⁵	a	r
0.70	3.100	0.998					−5.223	0.60	3.129	0.998
2.19	2.803	0.998	−4.862	1.37	2.976	0.999	−4.824	1.50	2.980	0.998
							−5.399	0.40	3.196	0.997
36.60	2.360	0.950	−4.703	1.98	2.909	0.995	−5.012	0.97	3.035	0.999
6.12	2.686	0.992	−4.805	1.56	2.944	0.997	−5.011	0.97	3.028	0.999
2.66	2.857	0.996	−4.654	2.22	2.891	0.956	−5.616	0.24	3.307	0.991

s e v, personal communication), which ensures an imporved food base in the rivers, while the remaining rivers are xenosoprobic (Y a n e v a, 1979, R o u s s e v and Y a n e v a, personal communication). One of the reasons for the comparatively slower growth rate of trout in the Vit river can be seen in the highest numbers of trout there — a mean value of 1768 specimens per ha, while the same value in the Chaya drainage area, where trout shows the highest growth rate, is only 530 trout per a. (Y a n k o v, 1987). Also our observations showed, that the difference in the growth rate of trout in various drainage areas are linked to the size, and above all the depth of the river, the intensity of angling and other causes.

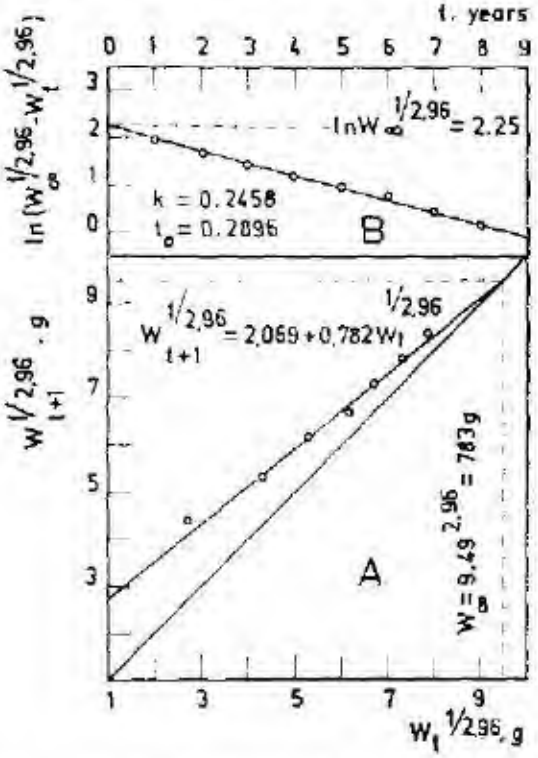

Fig. 2. Walford graph for length growth of brown trout in the Vacha drainage basin. A — Relationship between body length of trout at t age (L_t) and at t + 1 age (L_{t+1}). B — Relationship between age (t) and ln ($L_\infty - L_t$); L, k, t_0 — parameters of Bertalanffy's equation.

Linear growth of brown trout in the studied rivers is well described by the equation of Bertalanffy (see the position of plotted empirical points on the line in Fig. 2, A, and the values of coefficients of correlation and mean error in Table 5). It is evident from the same table, that coefficient k which according to some authors is an index of the rate of the growth of the population, has the highest values in the Chaya, Vit, and Struma drainage areas, despite the fact that in the Vit and Struma rivers trout growth is slower. This is explained

Table 4. Back-calculated average values of body lengths, mm (in numerator) and corresponding absolute annual increments (in denominator) of brown trout in different drainage basins

drainage basins	age, years 1	2	3	4	5	6	7	8	n
Chaya	103 / 103	186 / 83	236 / 50	260 / 24	289 / 29				101
Vacha	115 / 115	183 / 68	225 / 42	264 / 39	287 / 23	312 / 25	334 / 22	356 / 22	783
Iskar	116 / 116	174 / 58	208 / 34	235 / 27	271 / 36	305 / 34			138
Mesta	106 / 106	165 / 59	199 / 34	235 / 36	262 / 27	297 / 35	322 / 25		713
Struma	101 / 101	151 / 50	184 / 33	233 / 49	252 / 19	270 / 18			769
Vit	94 / 94	137 / 43	178 / 41	209 / 31	225 / 16				704

by the fact that the size of k is determined not only by the growth rate of the population, and moreover not to that extent by the growth rate, but also by the number of age groups in it, i.e., by its age structure. The greater the number of age groups, the smaller the values of k. For instance in Vacha, with a population of 8 age groups, $k = 0.2352$ (Table 5), with seven age groups $k = 0.2654$, while with five age groups $k = 0.3370$. Hence coefficient k in the equation of Bertalanffy is not suitable for comparative studies of the growth rate of different populations with a different age structure. Moreover, calculations with it are much more complicated than the simple classification of populations according to their values of L (Table 4).

Table 5. Parameters of the equations $L_t = L_\infty (1 - e^{-k(t-t_0)})$ and $L_{t+1} = a + bL_t$ (see Fig. 2) described length growth of brown trout in different drainage basins (r — correlation coefficient; S_D — standard deviation)

drainage basin	L_∞, mm	k	t_0	r	S_D, %	a	b	Number of specimens
Chaya	320	0.4736	−0.2386	0.997	4.37	120.538	0.623	101
Vacha	410	0.2352	−0.3349	0.998	3.14	85.927	0.790	783
Iskar	454	0.1623	−0.7783	0.996	3.62	68.000	0.850	138
Mesta	454	0.1604	−0.6212	0.998	3.14	67.224	0.852	713
Struma	346	0.2330	−0.4989	0.996	3.12	72.079	0.792	768
Vit	297	0.2607	−0.4840	0.998	2.40	68.203	0.771	704

We established age differences in the increase of mean weight of fishes (W), as related to their lengths (L). The coefficients k and n in the equation $W =$

$= kL^n$ ($lgW = lgk + n \cdot lg\,L$), describing this relationship, has various values with different age groups (Table 3). For instance the values of n vary from 2.360 to 3.640, i.e., by over one unit. It is generally considered that n = 3, which does not reflect the real regularity in the change of W as related to L. This is also special importance for the method employed — for instance in the study of the coefficient of condition. We consider that the coefficient of Fulton does not give a correct idea of the coefficient of condition. The correct

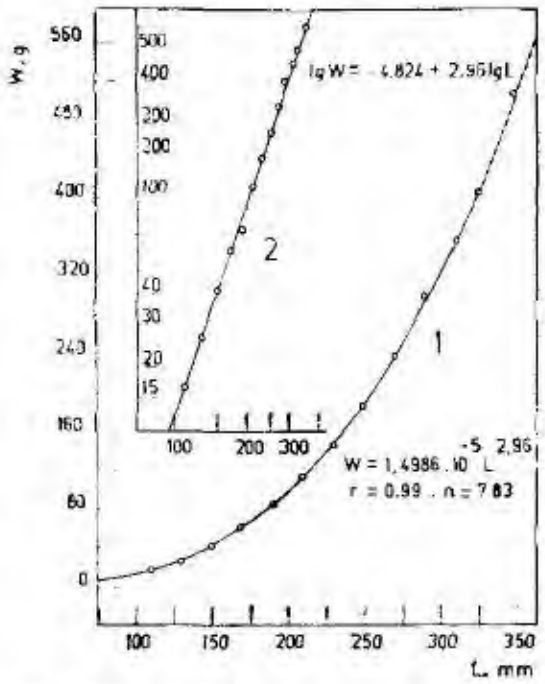

Fig. 3. Relationship between body length (L) and weight (W) (1) and its logaritmic transformation (2) of brown trout in the Vacha drainage basin.

value is obtained if the coefficient k from the equation $W = kL^n$, is used directly as a coefficient, computed for each age group separately. Thus Table 3 points to a tendency of an increase of the age of fish up to 3+, in all rivers (with the exception of Chaye river) as well as an increase of coefficient of condition. With fish at the 1+age from the Vit drainage area, where the growth rate was slowest, it shows the lowest value (Table 4).

If the relationship between W and L is described by one and the same equation for the whole population (Fig. 3 and Table 3), coefficient k in it may also serve as an index of coefficient of condition for various populations. It is evident from Table 3, that k has the highest value in Vacha — 1.50, while its lowest value is in the Vit river — 0.24, which is in accordance with the growth rate of river trout in these drainage areas. Fish from the Mesta and Struma have the same coefficient of condition.

Table 6. Back-calculated average values of body weights, g (in numerator) and corresponding absolute annual increments (in denominator) of brown trout in different drainage basins

drainage basins	age, years 1	2	3	4	5	6	7	8	n
Chaya	12	75	160	216	300				101
	12	63	85	56	84				
Vacha	19	79	140	221	283	363	445	538	783
	19	60	61	81	62	80	82	93	
Iskar	16	60	106	152	235	367			138
	16	44	46	46	83	132			
Mesta	13	54	97	155	215	308	390		713
	13	41	43	58	60	93	82		
Struma	11	39	74	145	183	225			769
	11	28	35	71	38	42			
Vit	8	32	71	113	140				704
	8	24	39	42	27				

Classification of growth throught weight of the population in decreasing order growth in weight (Table 6), coincides with their classification in Table 4. Contrary to linear annual increments values, which were largest during the first year (Table 4) growth through weight increments during this period was lowest (Table 6). During the second year the jump in the increase of weight increments was highest. After that this tendency was much weaker.

Table 7. Parameters of the equations $W_t = W_\infty (1 - e^{-k(t-t_o)})^n$ and $W_{t-1}^{1/n} = a + bW$ *(see Fig. 4 and Tab. 5); n — parameters from the equations in Tab. 3*

drainage basin	W_∞, g	k	t_o	n	r	S_n, %	a	b	Number of specimens
Chaya	414	0.4689	+0.2268	3.126	0.996	3.87	2.573	0.626	101
Vacha	783	0.2458	−0.2896	2.960	0.996	3.62	2.069	0.782	783
Iskar	1300	0.1636	−0.7378	3.196	0.994	4.06	1.423	0.849	138
Mesta	872	0.1921	−0.4530	3.035	0.997	3.33	1.627	0.825	713
Struma	445	0.2493	−0.4184	3.028	0.996	2.69	1.658	0.779	769
Vit	252	0.3496	−0.2630	3.307	0.999	1.58	1.570	0.705	704

A close relationship which follows the equation of Bertalanffy, is observed between mean weights (W) and age (t), as is evident from Fig. 4 and Table 7. However similar conclusions can be drawn about the parameters of the equation, describing linear growth. Thus coefficient k (rate, index of growth) of the population of Vit is larger than that of other populations with the excep-

tion of the population of the Chaya river) in spite of the fact that trout in the Vit has the lowest growth rate (Table 6). The values of the coefficients k and b ob the populations from Vacha and Struma are one and the same (Table 7), in spite of the great difference of their absolute growth in weight (Table 6). it is also noteworthy that with one and the same value of k and b, the values of W∞ in both drainage areas are almost doubled (between k and W∞, (L∞) should be inversely proportional). Purely graphically this could be explained and illustrated if next to the line of weight growth of fish from Vacha from Fig. 4, A we plot the data for the Struma. We will obtain a line, parallel

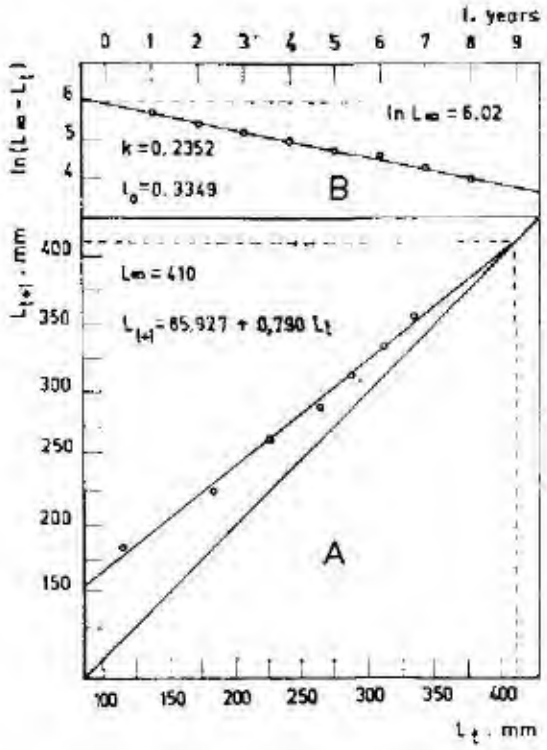

Fig. 4. Walford graph for weight (W) growth of brown trout in the Vacha drainage basin. Symbols as in Fig. 2; 2.96 — parameter from equation in Fig. 3.

to the first, running under it, hence it naturally will cut the bisector much lower, i.e. the W∞ value for Struma will be much lower. Biologically this phenomenon is explained with the larger mean values of the Struma river during the first and the second year (respectively 11 and 39 g) in comparison with the mean values of the weight of the population from the Vacha river (respectively 19 and 79 g.) for the same period and in spite of the almost identical further relative growth rate (k) with both populations.

Hence the value of W∞ is determined not only by the values of k (growth rate) or the slope (b) of line A (Fig. 4), but also from the values of the mean

"starter" weight. A similar conclusion can be made for L_∞. These observations should b etaken into consideration when we examine the biological meaning, assessment and application of the parameters of the equation of Bertalanffy.

The growth rate of trout from the Chaya and Vacha river basins is the highest and that of the Vit river the lowest. It is determined by water hardness and saprobity, population numbers, river depth and intensity of angling. Linear and weight growth are well described by the equation of Bertalanffy. However, coefficient k from the equation is not suitable for comparative analysis of populations of different ages. Our method of comparative analysis of populations of different ages is simpler and more precise. Considerable differences in growth of length of the body (L), correlated to (R), scale radius, and weight (W), in different age groups have been observed. However, if this is not taken into consideration in our method, in back calculations of L by R, and W by L would result in serious errors. The true condition of fish is only obtained if the value of the coefficient of condition is based on coefficient k from the equation $W = kL^n$, calculated for each age group.

SUMMARY

The growth rate of trout in the rivers studied was compared with that of another 120 rivers in the entire areal of the species. The comparison was carried out as is described and discussed with the compiling and of Tables 4 and 6. It has been established tha the mean data for the linear growth of trout in the rivers studied in Bulgaria and in those in Greece, Turkey and Macedonia do not differ substantially. The position of trout in England and Ireland, as well as Scotland and Wales is identical. Hence the comparative analysis of such regions, seen as a whole. It was established, that up to the third year trout in rivers in New Zealand show the highest growth rate, while the lowest was in Finland. The classification of the remaining countries in decreasing order according to growth rate was a follows: the USA, England and Ireland, the Balkan Countries, Czechoslovakia, Scotland and Wales. In higher age groups, however, the growth rate of trout in rivers in the USA is considerably greater than in comparison with the remaining rivers. Here the list runs as follows: England, Ireland, Czechoslovakia, Scotland and Wales, the Balkan countries, Finland.

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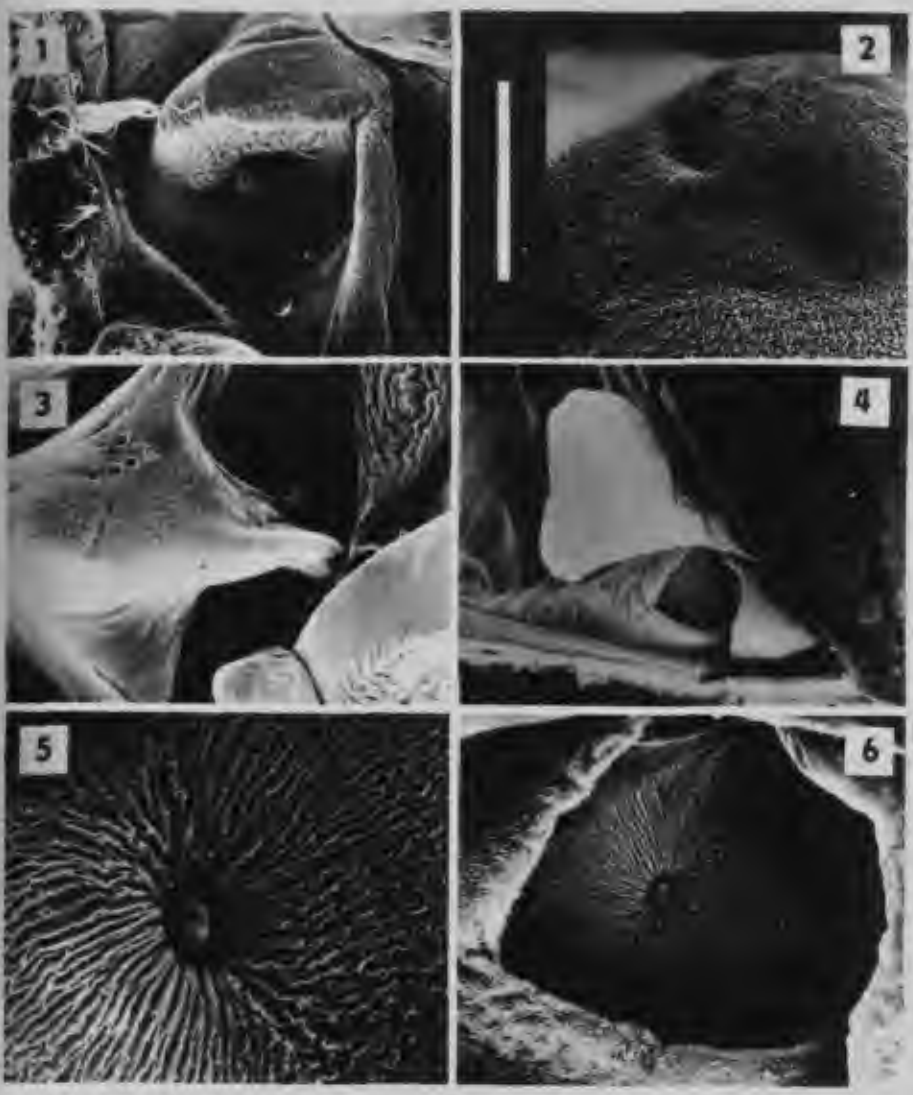

Plate 1. *Helotrephes semiglobosus* (Figs. 1—3) and *Trephotomas compactus* (Figs. 4—6). 1 — Region of mesothoracic scolopophorous organ; lateral view of the left side of body. Scale = 96 μm. 2 — Region of the metepimeron and scolopophorous organ of the 1st abdominal segment; lateral view of the left side of body. Scale = 162 μm. 3 — Forewing-anchoring knob of metepimeron; ventrolateral view of the left side of body. Scale = 35 μm. 4 — Thoracico-abdominal junction in the region of the scolopophorous organ of 1st abdominal segment; lateral view of the right side of body. Scale = 162 μm. 5 — Chamber of the scolopophorous organ of the 1st abdominal segment; lateral view of the right side of body. Scale = 33 μm. 6 — Scolopophorous organ of the 1st abdominal segment in detail. Scale = 8 μm.

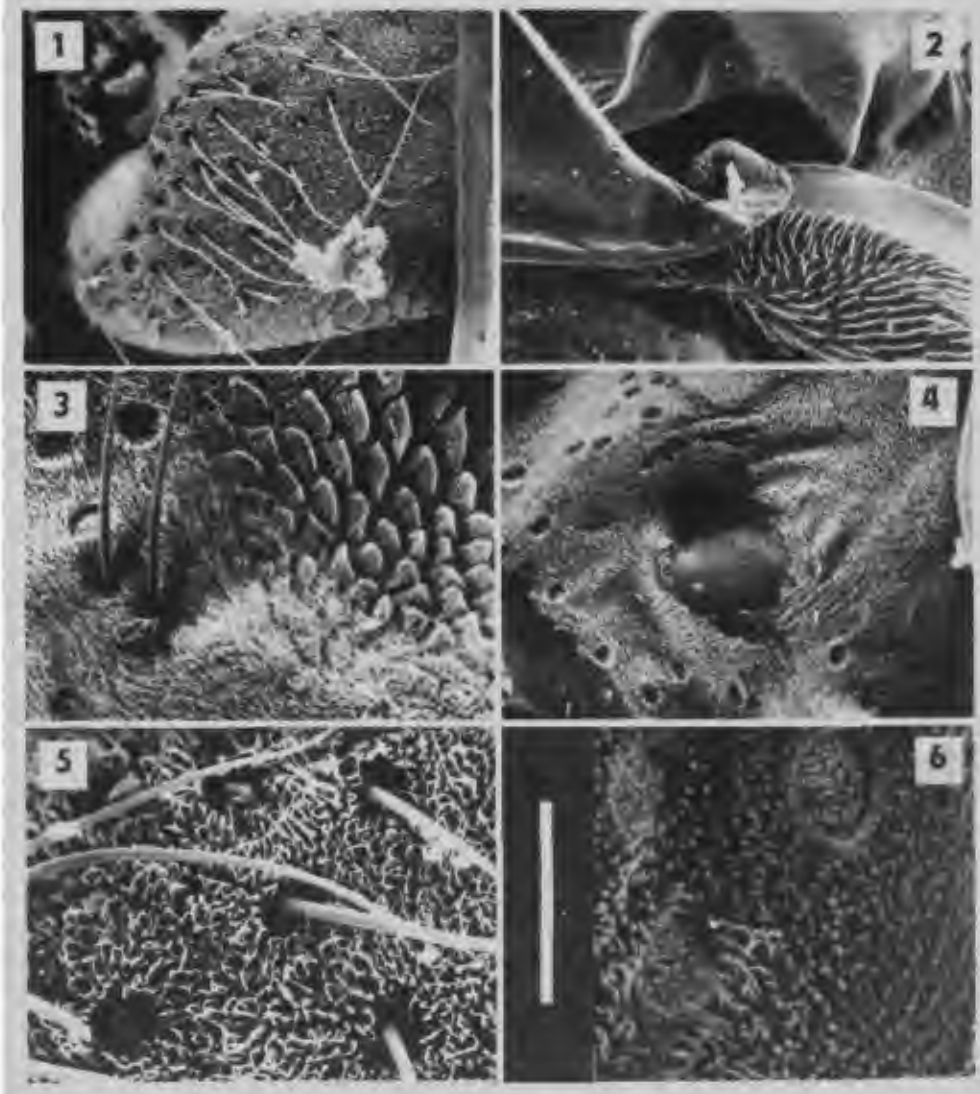

Plate II *Helotrephes semiglobosus* (Figs. 1—6). 1 — Anterior process of mesepimeron, ventral view of the left side of body. Scale = 68 μm. 2 — Wing-anchoring knob of the posterior corner of ventral mesepimeral lobe; lateral view of the left side of body. Scale = 130 μm. 3 — Lateral part of mesepisternum in the region of stridulatory apparatus; ventral view. Scale = 60 μm. 4 — Anterolateral region of mesepisternum; ventral view. Scale = 120 μm. 5, 6 — Main types of pilosity of the ventrolateral thoracic area. Scale = 34 μm (Fig. 5), = 27 μm (Fig. 6).

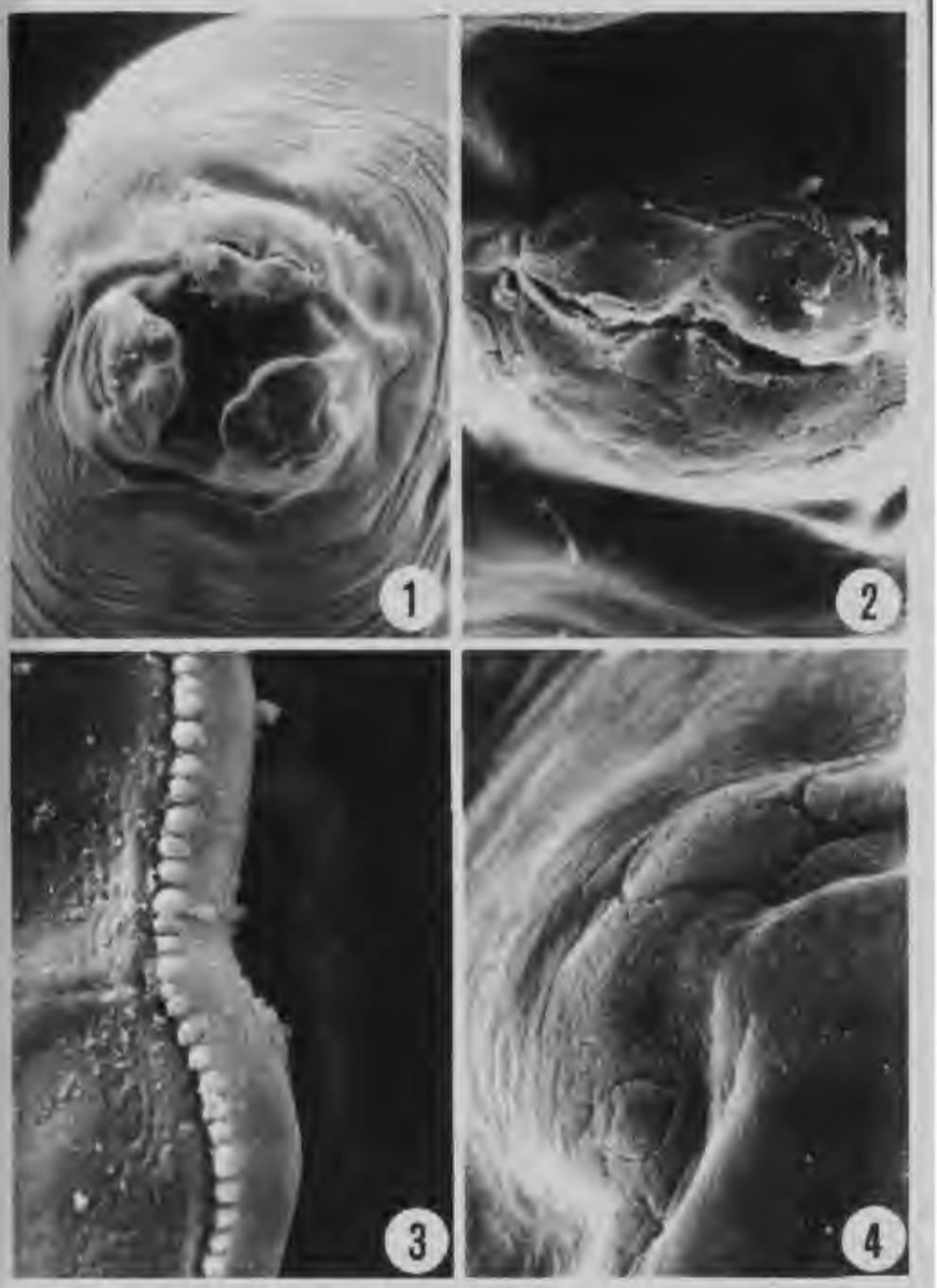

Plate 1. *Ascaris tarbagan* Schulz, 1931. **Fig. 1.** Head with three lips (× 150). **Fig. 2.** Dorsal lip, detail (× 450). **Fig. 3.** Denticles on the lip, detail (× 1800). **Fig. 4.** Doubled and single papillae on the latero-ventral lip (× 1200).

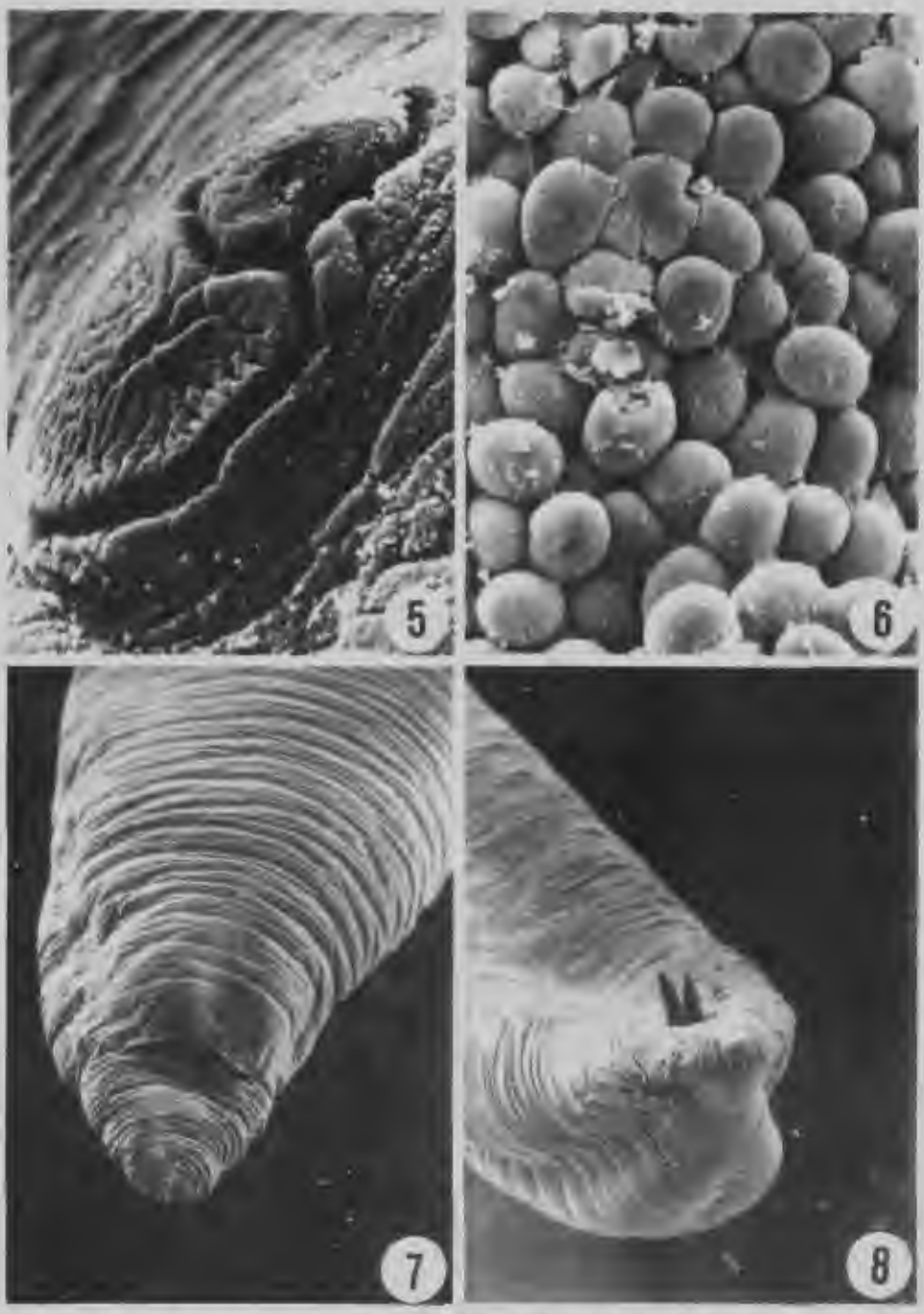

Plate II. *Ascaris tarbagan* Schulz, 1931. Fig. 5. Doubled papila on the dorsal lip (× 2400). Fig. 6. Eggs (× 360). Fig. 7. Abdominal end of female (× 60). 8. Abdominal end of male (× 90).

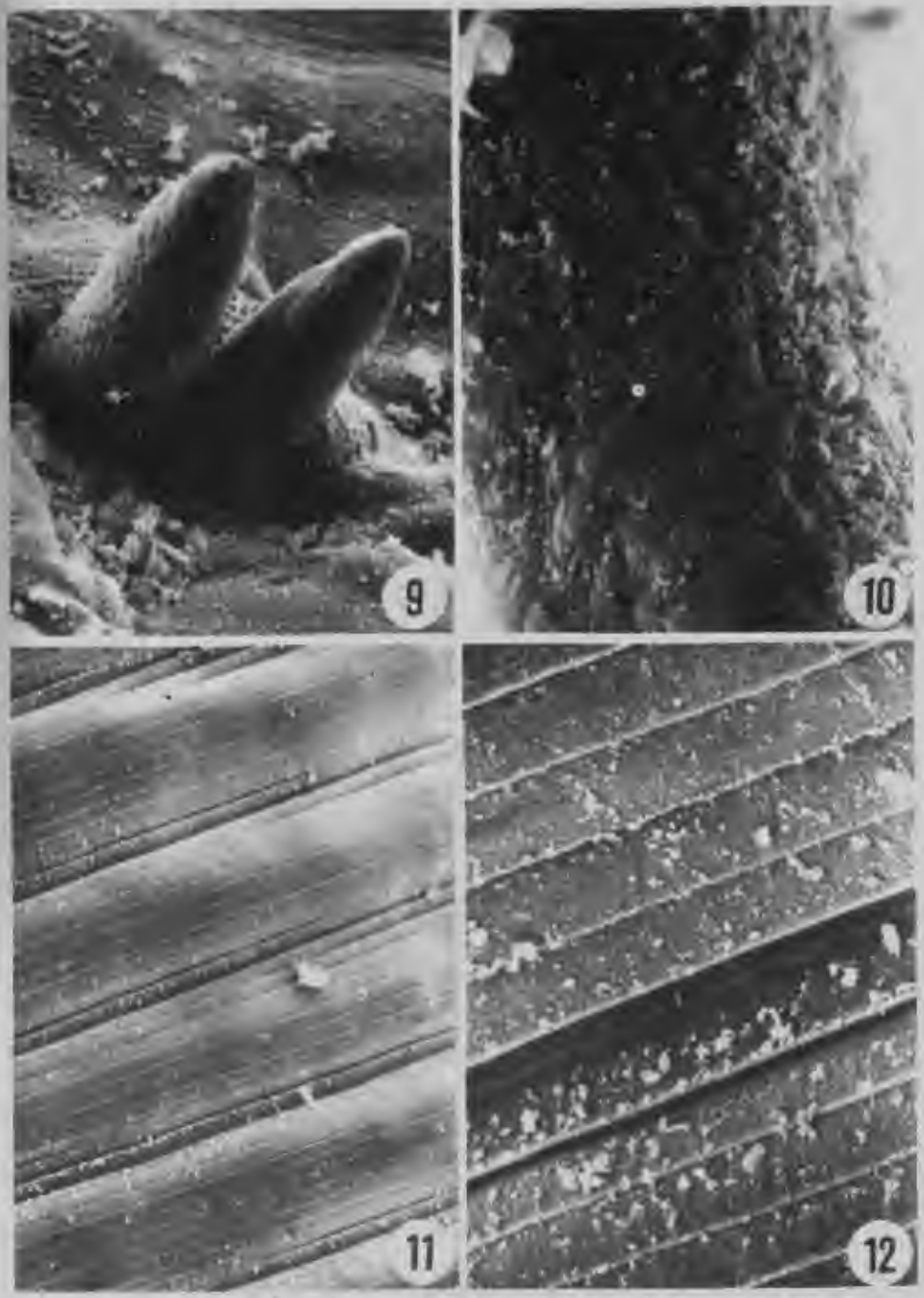

Plate III. *Ascaris tarbagan* Schulz, 1931. Fig. 9. Spiculae (× 660). Fig. 10. Surface of the spiculae (× 2400). Fig. 11. Surface of the body (× 420). Fig. 12. Surface of the body, detail (× 2400).

collis and Microtus agrestis

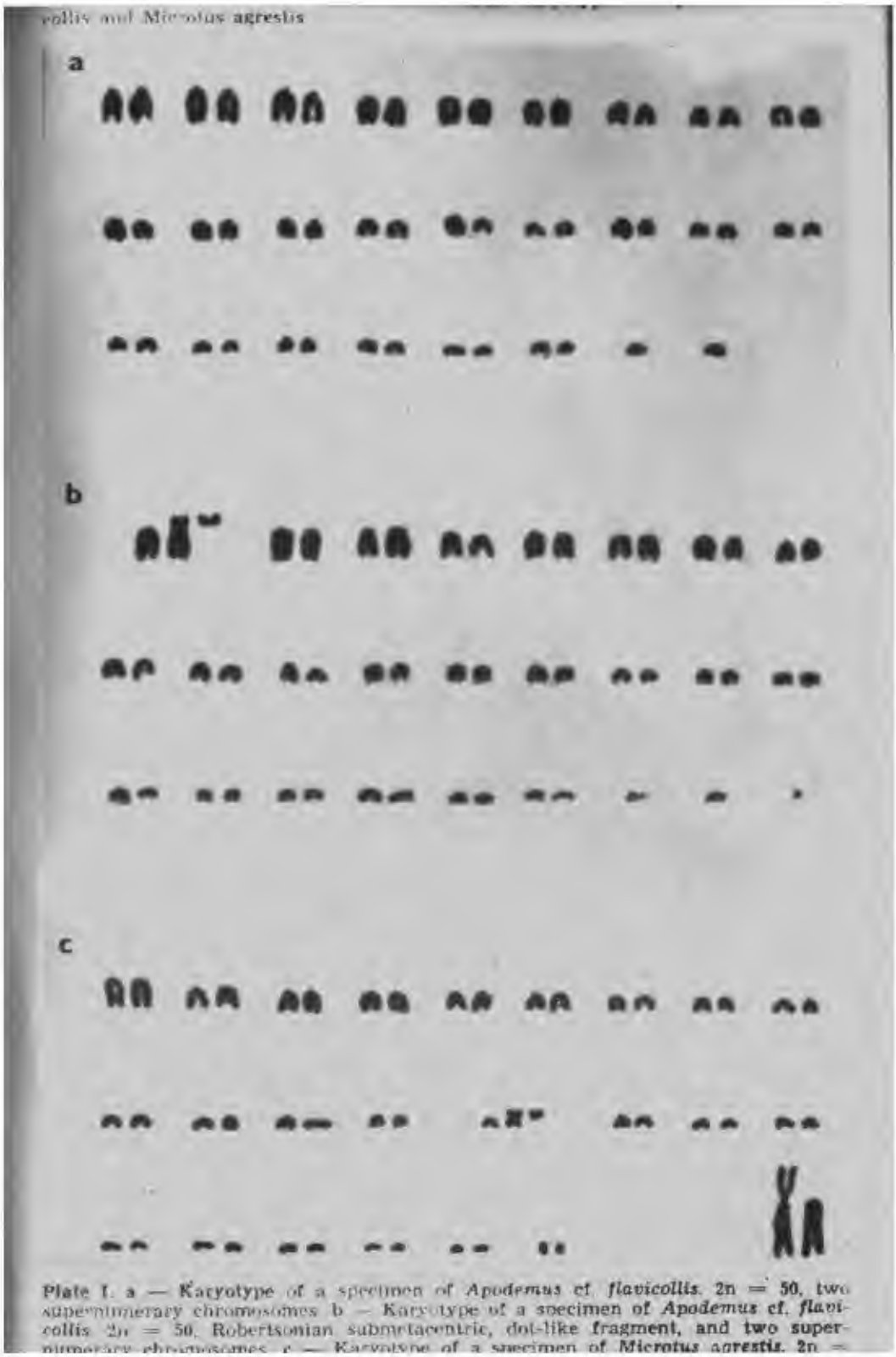

Plate I. a — Karyotype of a specimen of *Apodemus* cf. *flavicollis*, 2n = 50, two supernumerary chromosomes. b — Karyotype of a specimen of *Apodemus* cf. *flavicollis*, 2n = 50, Robertsonian submetacentric, dot-like fragment, and two supernumerary chromosomes. c — Karyotype of a specimen of *Microtus agrestis*, 2n =

INSTRUCTIONS TO AUTHORS

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